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FOREWORD

THE COMMONWEALTH INSTITUTE OF BIOLOGICAL CONTROL has an increasing number of scientific papers, technical notes and reports which it is often impossible to have published speedily in the usual journals, particularly when these contributions are lengthy or are in the form of interim reports. However, the information contained in these is often of immediate value in connection with the biological control problems involved and also of interest to other countries with the same or similar problems. It was felt desirable therefore to make an effort to provide such information as promptly as possible in the form of a publication more readily available and with a greater circulation than would be feasible with typewritten reports. This TECHNICAL BULLETIN OF BIOLOGICAL CONTROL No. 1 incorporates three papers which it is hoped will be of interest. If this is well received then further Bulletins will follow in due course.

I would be most grateful for criticisms and suggestions as to how these Bulletins might be improved.

F. J. SIMMONDS,
Director,
Commonwealth Institute of Biological Control

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A COMPARATIVE ANALYSIS OF THE PARASITE COMPLEXES OF THE EUROPEAN FIR BUDWORM, *CHORISTONEURA MURINANA* (HUB.) AND THE NORTH AMERICAN SPRUCE BUDWORM, *C. FUMIFERANA* (CLEM.)

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IX. Literature

I. Introduction

Much information on the parasites of the European fir budworm, Choristoneura murinana (Hub.), and the closely related North American spruce budworm, C. fumiferana (Clem.), has become available in recent years. Numerous investigations carried out at various places and with different host densities have indicated a fairly high constancy of the more important elements in the parasite complex of C. murinana (CAPEK et al., 1958), and also in that of C. fumiferana (McGUGAN & BLAIS, 1959). Moreover, a certain similarity of the parasite complexes of the European and North American Choristoneura species has been pointed out (BUCHER, 1953; FRANZ, 1957; CAPEK & ZWOLFER, 1957). However, biocoenotic studies undertaken simultaneously on the parasitism of C. murinana and some other Microlepidoptera species of the same community (ZWOLFER & KRAUS, 1957; CAPEK, 1960) showed clearly remarkable differences in the parasite fauna of the fir budworm and some other lepidopterous species in the same habitat which might have been presumed to be potential hosts.

All these observations, the relative uniformity of both Choristoneura complexes, their apparent similarity to each other, and their differentiation from the parasite complexes of other host species, indicate that the composition of the parasite complexes of these insects is not merely an accidental result of coincidence in time and space of the parasite fauna of the communities concerned and suitable host species, but that certain additional requirements must be met for the establishment of such fairly regular systems.

Basic research involved in attempts at biological control of insect pests revealed similar facts in the parasite/predator complexes of other hosts and, thus, the existence of well characterized and relatively constant associations between entomophagous parasites and a given host species may be rather common. However, little attention has been paid to this often rather obvious regularity and characteristic composition of parasite-host associations. Whilst a vast number of publications analyze the means by which a single parasite species comes into contact with its potential hosts (literature cited by DOUTT, 1959) only very little interest has been taken in the question as to why a given host species is often associated with a characteristic and rather constant combination of parasite species.

Comparative investigations of parasite associations with insect hosts may be one of the ways to solve this question and to obtain a certain insight into the structure and evolution of such complexes. Therefore, an attempt has been made in the present study to evaluate the available observations on the parasites of C. murinana from the view-point of their position within the complex, their relative constancy and abundance, their general host relationships and ecological limitations, and to compare thesingle parasite species of the European C. murinana with those of the North American C. fumiferana with regard to their taxonomic relationships, their ecology, host-range, relative constancy, and abundance. The data presented in this comparison may offer a certain interest per se, since both parasite complexes are connected with economically

important insect pests, and repeated trials have been undertaken to improve the controlling effect of the North American spruce budworm parasites by the introductions of European fir budworm parasites. The main object of the present study was, however, to apply some principles of general comparative parasitology to the special case of entomophagous parasite (parasitoid) associations of systematically and ecologically related, but geographically separated, host species, and to consider in this way the problem of the establishment and evolution of insect parasite complexes.

Acknowledgements.

Most of the present observations on the parasites of the fir budworm have been made during mass-collections carried out by the European Station of the Commonwealth Institute of Biological Control during the years 1955 to 1958. I am obliged to Dr W.R. Thompson, former Director of the CIBC, who enabled me to start the investigations, and to undertake complementary observations after the mass-collections of the fir budworm had finished, and I am also much obliged to Dr F.J. Simmonds, present Director of the CIBC, who allowed me to finish this study and who has kindly gone through the manuscript. The evaluation of the data was carried out at the European Station, Delemont (Switzerland), under the supervision of Professor L.P. Mesnil, Entomologist-in-Charge. I am much indebted to Professor Mesnil for the interest he has taken in these investigations, for his comments on problems concerning Tachinids, and for his many suggestions. I have also to thank my friends Dr H. Pschorn-Walcher (CIBC) and Dr M. Capek (Banska Stiavnica, CSR)

for discussions and criticism. Dr Capek also communicated to me his interesting observations on parasites of the fir budworm and other forest Tortricids in Slovakia. The following specialists were kind enough to identify parasite material reared or to give me valuable information in this field: Dr R. Bauer, Nuremburg; Dr V. Delucchi, Rabat (Morocco); Dr Ch. Ferriere, Geneva; Dr W.R. Mason, Ottawa; Dr G.E.J. Nixon, Dr G.J. Kerrich, Commonwealth Institute of Entomology and Dr J.F. Perkins, London; Dr R. Hinz, Einbeck (Germany). Dr Mason was most kind in sending me a shipment of identified parasite species reared from the spruce budworm. With this generous gift a morphological comparison of the fir and spruce budworm parasites was possible. I have also to thank Dr B.P. Beirne, Belleville, Ontario (Canada), who sent me an identification list of the fir budworm parasite material shipped to Canada in 1956.

II. Material and methods

The first section of this paper deals with the composition of the parasite complex of C. murinana and the biology and ecology of the parasites concerned. There follows a comparison between various aspects of each of the individual parasite species and those of their counterparts in the complex of C. fumiferana. Finally there is a discussion of these comparisons and their implications from the standpoint of general parasitology, biogeography and phylogeny.

The study of the parasite complex of C. murinana was based primarily on the following material (round figures):

1955: 12,000 host larvae (+ 300 larval parasites and 2,100 host pupae (+ 900 pupal parasites) from the Vosges (Ribeauville, Ht. Rhin, France).

1956: 240 larval parasites and 3,000 host pupae (+ 1,000 pupal parasites) from the Vosges.

250 larval parasites and 5,400 host pupae (+1,300 pupal parasites) from the southern Black Forest (Staufen, nr Freiburg/Brg., Germany).

330 larval parasites and 15,300 host pupae (+ 2,900 pupal parasites) from the northern Black Forest (Baden-Baden, Germany).

610 larval parasites and 4,000 host pupae (+ 460 pupal parasites) from central Slovakia (Banska Stiavnica, CSR).

1957: 130 host larvae (+ 20 larval parasites), 40 larval parasites, and 90 host pupae (+ 40 pupal parasites) from the Vosges.

750 host larvae (+ 160 larval parasites) and 300 host pupae (+ 140 pupal parasites) from the southern Black Forest.

1958: 420 host pupae (+ 100 pupal parasites) and several random samples of host larvae from the southern Black Forest.

Altogether the parasitism of more than 12,800 C. murinana larvae and more than 30,500 C. murinana pupae has been analyzed. 1,850 larval parasites and 6,810 pupal parasites have been obtained from these collections, rearings and dissections.

Collections of C. murinana material were obtained principally by climbing mature firs (Abies alba). However, some of the pupae and larvae were also collected from young firs in thickets, or from

the litter on the soil. Host material was separated according to the date, the locality and ecological conditions of each collection, the age of the host plant, and the population density of C. murinana. Sixty samples, each containing 50-100 hosts were separated and kept under daily observation. The degree of parasitism of the larval population was calculated separately on the basis of dissections of third and fourth larval instars, and that of the pupal population on a basis of a combination of rearings and dissections of smaller samples, which had been taken just prior to the commencement of the emergence of the adult fir budworms. Earlier collections of pupae were found to give unsatisfactory results (ZWOLFER & KRAUS, 1957), since in general a considerable increase of parasitism takes place during the early pupal period.

In addition to the rearings of fir budworm an attempt was made to obtain as much information as possible as to the bionomics and ecological relationships of its parasites by direct field observations, by field collections of parasite adults, by rearings of potential hosts occurring in the same community, and by laboratory observations on the behaviour of the parasite adults. Much information was also derived from discussions with other entomologists. The author is greatly indebted to all his colleagues (Dr Baltensweiler, Zurich (Switzerland); Dr Capek, Banska Stiavnica (CSR); Dr Bauer, Nuremburg (Germany); Dr Auersch, Halle a.S. (Germany); Dr Schutte, Darmstadt (Germany), etc., all of whom provided various observations on individual parasite species. During several visits to Banksa Stiavnica (CSR) the author had the opportunity to compare the

parasite species reared in the Vosges and in the Black Forest with the extensive parasite material which Dr Capek had obtained from both C. murinana and other forest Microlepidoptera in Slovakia. Thanks to the continuous cooperation of Dr Capek it was possible to check my own observations and conclusions as to the ecology of several parasite species, and to obtain a broader basis for this study.

Information on the parasites of C. fumiferana was obtained from the literature cited on page 65.

Thanks to a generous gift by Dr Mason, Ottawa, comprising all the important and characteristic hymenopterous parasites of C. fumiferana, and thanks to detailed information from Prof. Mesnil, Entomologist-in-Charge, European Station, Commonwealth Institute of Biological Control, on the dipterous parasites, a morphological comparison of the species occurring in the two Choristoneura complexes was possible. Special interest was taken in the problem of the morphological relationships between the parasites of C. murinana and the corresponding North American species on C. fumiferana, as compared with the relationships of both these complexes and those of other related European forms. Since the reference collection of the European Station provided only a very incomplete basis for this comparison, Dr Kuhlhorn of Munich was asked for the loan of identified European Ichneumonid species from the collection of the Bavarian State (Munich). In this way a large amount of material was obtained for our comparative study and a great number of European species of the genera concerned could be examined, especially among the

Pimplini* and Ephialtini* which are relatively well represented in the Choristoneura complexes.

III. Remarks on the two host species

The fir budworm, Choristoneura murinana, is taxonomically more closely related to the North American spruce budworm, C. fumiferana, than is any of the other European Tortricids. This close systematic relationship between the two species is reflected in a great similarity in their larval and adult morphology, biology, and ecology. (BUCHER, 1953; FRANZ, 1957; WITTIG, 1959).

Distribution

The present distribution area of C. murinana comprises parts of northern and eastern France, southern and central Germany, Switzerland, Austria, CSR, southern Poland, northern Italy and north-western USSR (PATOCKA, 1960). Recent outbreaks have been observed in the Vosges, the northern and southern Black Forest, the Swiss Jura, the Vienna Forest, central Moravia, and central and east Slovakia. The main outbreak localities of C. murinana are situated along the edge of the northern part of the natural distribution area of its host plant, Abies alba.

C. fumiferana occurs in eastern North America (Canada: Newfoundland, Nova Scotia, New Brunswich, Quebec, Ontario; U.S.A.: Maine, New York) as well as in western North America (Canada: British Columbia, Alberta; U.S.A.: Oregon, Montana, Idaho, Colorado,

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*The material was checked and reidentified by Dr Perkins, British Museum, London.

New Mexico).

The area of distribution of C. murinana covers a region with a warm summer and a relatively mild winter climate. Winter temperatures within the areas occupied by C. fumiferana are considerably lower. Fig. 1 shows the range of monthly average temperatures in areas inhabitied by C. murinana (eastern France, western Germany, eastern Austria, CSR, Poland) and C. fumiferana (Quebec, Ontario, New Brunswick, Maine, New York, British Columbia) (MORGENTHALER, 1952). In these areas rainfall occurs throughout the whole year; however, the summer period in British Columbia is comparatively dry. The yearly averages are 660-990 mm. (= 260-400 inches)(areas of C. murinana); 810-1060 mm. (= 320-420 inches) (north-eastern American areas of C. fumiferana), and 700-2100 mm. (= 280-840 inches)(British Columbia).

Host plants

C. murinana feeds virtually only on silver fir, Abies alba. Other coniferous hosts (Picea abies, Larix decidua, etc.) may sometimes be attacked as a result of mass outbreaks, but are normally of no importance to the fir budworm.

C. fumiferana has a more diversified host range. The main host plants are balsam fir, Abies balsamea, white spruce, Picea glauca, red spruce, P. rubens, and black spruce, P. mariana, in eastern Canada and U.S.A., and Douglas fir, Pseudotsuga taxifolia, alpine fir, Abies lasiocarpa, and Engelmann spruce, P. engelmanni, in British Columbia and the Canadian Rocky Mountains. C. pinus Free.,

a species very closely related to C. fumiferana, attacks Jack-pine, Pinus banksiana (Ontario, Michigan).

Biology

Oviposition of both C. murinana and C. fumiferana takes place in midsummer on the needles of their host plants. The incubation period generally lasts between one and two weeks. On hatching the larvae seek places for hibernation on the host tree (mostly cracks in branches and twigs, etc.) and there form small hibernacula. Within these they moult. The autumn and winter are passed in diapause in the second larval instar. The feeding period starts in spring about the same time as the buds of the host plant are beginning to burst. The larvae attack staminate flowers and buds and needles of the younger shoots. There are six larval instars. Pupation occurs in late spring or early summer. Most of the pupae are formed in the crown region. Adults emerge following a pupal period of from one to two weeks.

Economic importance

PATOCKA (1960) considers C. murinana as one of the most important insect pests of mature silver fir. The species shows a tendency towards periodic outbreaks which may last up to ten years. These outbreaks are often accompanied or followed by the attack of other fir insects such as Zeiraphera rufimitrana H.S., Epinotia nigricana H.S., etc. They usually cause severe damage to, or the death of, the trees infested. The heaviest attack by C. murinana is shown in fir stands growing at the border zone of the ecological range of Abies alba,

i.e. at sites which are normally occupied by oak-beech or oak-hornbeam forests (Fageto-Quercetum, Carpineto-Quercetum). It is here that outbreaks usually develop, and here also that the heaviest losses are to be expected (FRANZ, 1957; PATOCKA, 1960).

C. fumiferana is "by far the most destructive defoliator in Canada" and parts of the U.S.A. "and its periodic outbreaks constitute major forest disturbances". The mass outbreaks of C. fumiferana "seem to be a part of the natural cycle of events associated with the maturing of extensive forests of balsam fir" (MORRIS et al., 1956). Enormous quantities of trees are killed during such calamities, which occur to a large extent within the natural optimum of the balsam fir.

Differences between C. murinana and C. fumiferana

C. murinana is virtually restricted to a single host plant, whilst C. fumiferana attacks a number of coniferous species other than Abies.

The geographical distribution area of C. murinana is comparatively small and relatively continuous. No special races or sibling species are known to occur in Europe. C. fumiferana, on the other hand, covers much greater, but widely separated, areas on the North American continent and the species appears to be less uniform than C. murinana. There exists, for instance, in the Canadian Rocky Mountains (SHEPHERD, 1959) a form with a two-year cycle, and also a very closely related species on Pinus banksiana (C. pinus).

Outbreaks of C. murinana are relatively local and occur mainly

outside the optimum growth area of the host plant. Outbreaks of C. fumiferana, however, may affect immense areas within the ecological optimum area of the host (FRANZ, 1957).

Finally a comparatively small difference between the larval feeding habits of the two species which may, however, exert a considerable influence on the survival rates of the larval populations (FRANZ, 1957) may be mentioned here. During the beginning of their activity in spring the second instar larvae of C. murinana can feed only within bursting buds. The larvae of C. fumiferana, however, are also able to mine in old needles and in unopened buds, and are thus less dependent on seasonal coincidence with the development of the host plant.

The differences between these two species of Choristoneura as outlined above are certainly of some importance, but are not sufficient to offset the close similarity of the two species and the very marked correlation which is evident in their taxonomic position, behaviour and general ecology.

IV. Parasite complex of C. murinana

(A) Parasite species

(1) Dominant species

(a) Cephaloglypta murinanae (Bauer)(Ichneum.-Glyptini)
(Glypta murinanae Bauer; Cephaloglypta excavata Obrtel)

Material: ca 1000 individuals

Life history: Only one generation per year. Imaginal period: July. Oviposition occurs soon after the emergence of C. murinana larvae

(generally second half of July). During the remainder of the season the parasite remains in diapause within the hibernating host larva, probably in the second larval instar (the early third instar of the parasite has been found in dissections made at the beginning of the feeding season of the host larvae (April 1, 1957 - Staufen)). After further development of about five or six weeks within the host larva, the host is killed in its sixth (last) instar, and left by the full-grown parasite larve (generally second half of June). For pupation the parasite larva spins a transparent thin cocoon (ca 12 x 5 mm.) on the needles or on the twigs of the infested fir; occasionally it may move prior to pupation to the litter on the ground. Pupation occurs in 3-4 days. Pupal period: 16-20 days. Soon after emergence (first half of July) mating takes place. Average longevity of adults under laboratory conditions: ♂♂ 10 days, maximum 36 days; ♀♀ 35 days, maximum 71 days (BUCHER, 1948). The ratio of ♀♀ to ♂♂ is fairly constant, ♀♀ always being somewhat more numerous (average of 781 individuals from the Vosges, the Black Forest, and Slovakia, 1956: 55/45).

Hyperparasites: The reduction of numbers through secondary parasitism varies widely (1956: Staufen 45%, Vosges 28%, Slovakia 14%; from a total of 944 Cephaloglypta cocoons 239 (= 25%) had been destroyed). The principal parasites are Itoplectis maculator (F.) and Monodontomerus aereus Walk., both also primary pupal parasites of C. murinana (ZWOLFER & KRAUS, 1957). Further hyperparasites: Pezoporus sp. (Vosges 1955), Gelis instabilis (Foerst.)(CSR 1956),

Dibrachys cavus (Walk.) and Copidosoma ? flagellare (Dalm.) (both Staufen and Baden-Baden, 1956).

Constancy and abundance: This highly specialised parasite species is practically always associated with C. murinana. Percentage of parasitism by C. murinanae in C. murinana: Vosges (1955) ca 5%, (1956) 6.8%, (1957) 6.4%; Staufen (1956) 0.9%, (1957) 1%; Slovakia (CAPEK et al., 1958) 2.2%.

Host-preferences

During my own investigations C. murinanae was found only on C. murinana, but Dr Capek has also reared this species from Archips piceana (L.) (on fir) and from A. sorbiana (Hb.) (on oak, situated on the border of a fir forest). According to my observations (Vosges 1955, 1956; Staufen 1956) the host is more heavily parasitized by C. murinanae in the crowns of mature firs (especially on warm and sunny slopes) than in fir thickets (the general ratio of the "cocoon per host" density for thickets and mature stands, both in comparable biotops, was 29:71 (Vosges 1955) and 33:67 (Staufen)). This indicates an ecological preference for the crown stratum of mature firs. It must be remembered, however, that after the attack of C. murinanae there may still occur a considerable spreading of the host larvae (FRANZ, 1940) which does not permit of an exact comparison in this way.

(b) Apanteles murinanae Capek & Zwolfer (Braconidae-Microgasterinae).

Material: ca 300 individuals

Life history: Only one generation per year. Imaginal period: June/July. Oviposition takes place soon after the emergence of the host larvae (generally second half of July). The parasites remain from late summer until next spring in diapause (as L_1) within the host larvae which are hidden in their hibernacula. Development only continues when the young host larvae (L_2) enter the growing fir buds (end of April, beginning of May). Host larvae are killed in the fifth (second last) instar*. Full-grown parasite larvae leave them for pupation within dense white oval cocoons (3-4 mm. in length) fastened between the fir needles, or onto the twigs of the tree. Duration of the pupal stage: 10-12 days. The main period of emergence (second half of June) is shortly before or at the same time as the emergence of the host. Mating takes place soon after emergence.

Average longevity of imagines under laboratory conditions: ♂♂ 10 days; ♀♀ 20 days, maximum 40 days (BUCHER, 1953). In all the observation areas ♂♂ were more abundant than ♀♀. Ratio of ♀♀ to ♂♂ in the Vosges (1956) 40:60, Staufen (1956) 31:69, Baden-Baden (1956) 21:79, Slovakia (1956) 35:65.

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*Dissections of host larvae (Staufen 1957) revealed a remarkable disparity in the development of the individual host larvae: during April only L_1 had been found, in the first half of May already L_2, L_3 and cocoons had been observed but L_1, on the other hand, were still present until the end of May. Occasional parasitism by this species on Z. rufimitrana (hibernating in the egg stage) is perhaps caused by those adults which develop from C. murinana during the first half of May.

Hyperparasites: Secondary parasites are important limiting factors. Apanteles cocoons destroyed were: Vosges (1955) 40%, (1956) 25%; Staufen (1956) 46%; Baden-Baden (1956) 45%. In addition to Amblymerus subfumatus (Ratz.) (punctiger Thoms.), which is also a primary parasite of C. murinana, the following species have been observed attacking A. murinanae: Gelis instabilis, Thysiotorus thomsoni Kerrich (= Leptocryptus aereus Thoms.), Hemiteles areator Panz., H. longicauda Thoms., Hemiteles sp. nr longicauda Thoms., H. albipalpus Thoms., Hemiteles sp., Habrocytus acutigena (Thoms.) (Vosges 1955/56, Black Forest 1956/1957).

Constancy and abundance: This highly specialized parasite seems always to be associated with C. murinana (see CAPEK & ZWOLFER, 1957). In the Vosges where C. murinanae was the dominant larval parasite in 1955-57, A. murinanae was rather rare: (1955) 0.25%, (1956) 0.4%, (1957) 4.8%. At Staufen A. murinanae was found to be more abundant than C. murinanae: (1956) 2-3%, (1957) 11%. In Slovakia Dr Capek indicated an average of 2.4%.

Host-preferences: The host spectrum of A. murinanae is somewhat broader than that of C. murinanae, but according to all observations so far made C. murinana holds the key position in this host list. Additional (occasional) host species have been found: Z. rufimitrana (Vosges, Slovakia), E. nigricana, Parasyndemis histrionana (Froel), Archips piceana (L.), Epinotia pusillana Pey. (all records from Slovakia by Dr Capek (personal communication)). All these hosts occur in forests on coniferous trees and they occupy in the

biocoenosis similar ecological niches to C. murinana. Since A. murinanae had never been reared from hosts with other ecological requirements, it seems justifiable to consider A. murinanae as a "woodland-form" with a marked preference for hosts on coniferous trees.

(c) Phaeogenes maculicornis (Steph.)(Ichneum.-Phaeogenini) (Phaeogenes scutellaris Wesm.)

Material: 600 individuals

Life history: The female oviposits in pupae, preferably freshly formed ones, of C. murinana (June). The larval and pupal periods together last 20-24 days. Emergence takes place in mid-July. Mating occurs shortly after emergence. Longevity under laboratory conditions: ♂♂ ca 2-3 weeks. Contrary to Bucher's observation (1953) fecund ♀♀ could be kept alive in the laboratory until the following spring. SEYRIG (1924) found overwintering ♀♀ of Ph. maculicornis frequently in forests under a cover of moss on trunks of old trees. In contrast to distinctly multivoltine pupal parasites such as Itoplectis, Pimpla and Apechthis, which may start oviposition a few days after emergence, the eggs of Ph. maculicornis are not yet developed in the ovarioles for a month following emergence. The species is able to overwinter in the adult stage and to maintain itself with only a single generation per year. However, an additional generation may occasionally occur, as with the related Phaeogenes nigridens Wesm. (SMITH, 1932). In most cases the sexes have been reared in about equal numbers, the ratio of ♀♀ to ♂♂ being: Vosges (1955) ca 50:50, (1956) 46:54; Staufen (1956) 29:71;

Baden-Baden (1956) 45:55.

Hyperparasites: Secondary parasitism by Monodontomerus aereus and Amblymerus subfumatus—both of which are also primary parasites of C. murinana—plays a minor role: Vosges (1956) 3%, (1957) 5%; Staufen (1957) 4%.

Constancy and abundance: The species is fairly constantly associated with C. murinana (Tab. 1). In its abundance, however, it exhibits much greater variations than any of the other parasites of C. murinana, as has already been stated by SCHIMITSCHEK (1943). In the Vosges (1955, 1956) the species was, with 20.6% and 22.8% parasitism, the most important pupal parasite, and in Moravia (SCHMITSCHEK, 1943), and recently in Poland (WIACKOWSKI, 1957a,b), it was also dominant. In the various rearings made of material from the Black Forest and Slovakia, however, Ph. maculicornis was either totally absent (FRANZ, 1940) or not very significant: Staufen (1956-58) 1-4%; Baden-Baden (1956) 1%; data of FRANZ et al. (1953): Baden-Baden (1956) 1.2%, Gernsbach (1956) 2.5%; Slovakia (own material)(1956) 0.5%. This disparity of abundance is apparently not due to geographical factors (vide the observations in the Vosges, Moravia and Poland).

Host-preferences: In addition to C. murinana, Ph. maculicornis has occasionally been reported as a parasite of Lepidoptera living on Larix: Zeiraphera diniana Gn. (JAHN, 1948) and Spilotana laricana Hein. (WIACKOWSKI, 1957a). There is also a record from Ptycholomoides aeriferana (H.S.)(Meyer, 1936). The parasite is a typical "woodland-

-form" which apparently shows a preference for insects on coniferous trees such as Abies and Larix.

According to our observations in the Vosges (1955, 1956) host pupae in the crowns of fir trees are more heavily attacked by Ph. maculicornis than those on young firs in thickets (ratio about 60:40).

(d) Itoplectis maculator (F.)(Ichneum.-Pimplini)(Pimpla maculator F.)

Material: 2,470 individuals

Life history: Oviposition takes place earlier in the season than with the other pupal parasites, partly in the last larval instar (L_6), partly in the freshly formed pupae. Sometimes the host larvae attacked are unable to pupate normally; they merely develop a brownish colour and become strongly chitinized. The larval and pupal periods together last 20-24 days. Emergence of adults occurs at the same time as that of the host. Mating takes place just after emergence. Longevity under laboratory conditions: ♂♂ 10-20 days, ♀♀ 30-40 days. (AUBERT (1959) observed a longevity of three months in the ♀♀ of Itoplectis sp.)

As had been shown by laboratory tests with material from the Vosges (1956) young females are able to oviposit two to three days after emergence on Galleria melonella (L), Acleris maccana Tr. and Ephestia kuhniella Z. (with the last-mentioned host only male offspring were obtained). Thus potentially I. maculator could have a further three to four generations before entering a winter diapause. However, under field conditions at most only a small part of the

I. maculator population may complete this number of generations, since in the observation areas the density of potential alternate hosts was very low compared with that of I. maculator. The period of flight (May-October, with two distinct maxima at May/June and September/October) indicates an average of two generations which more or less coincide with the two periods during which potential hosts are most readily available. (With regard to the problem of alternation of hosts see section IV(B)(4)). Hibernation of adult I. maculator has also been observed (a living female was found in late December 1957 on a young fir tree). Ratio of ♀♀ to ♂♂: Vosges (1955) 28:72, (1956) 40:60; Baden-Baden (1956) 50:50; Staufen (1956) 45:55; Slovakia (1956) 46:54.

Behaviour of adults: Adult parasites frequently feed at pre-oviposition punctures on host body fluids. In my rearings a considerable proportion of the "laboratory hosts" was killed in this way. Successful oviposition requires, in addition to olfactory stimuli, visual appreciation of, or at least tactile contact with, the host (laboratory tests with material from the Vosges (1956)). For this reason host pupae fully enclosed in a part of the host plant (for instance those of Rhyacionia buoliana (Schiff.)) seem to be precluded from parasitism by I. maculator.

Hyperparasites: Hyperparasitism by Monodontomerus aereus and Amblymerus subfumatus—both also primary parasites of C. murinana—played a minor role in the Vosges (1956 3%, 1957 5%) but was quite important at Staufen (1957 14% !).

Constancy and abundance: I. maculator is constantly associated with C. murinana and is, in general, considered the most important pupal parasite (Table 1, Fig. 1). Although I. maculator, as a multivoltine species, cannot follow exactly the population trends of the host, it is able during mass outbreaks of C. murinana to destroy up to 15% of the pupae (Vosges (1955)14.5%, (1956) 11.5%; Staufen (1956) 12.8%; Baden-Baden (1956) 11%) (FRANZ et al. (1958): Baden-Baden (1956) 18%; Gernsbach (1956) 10.8%). At lower host densities the parasite may become even more effective; at Staufen in 1956 where several stands of firs, each with a very different host-density, could be compared, we found at a high density of host pupae (100% destruction of the young shoots of fir) a parasitism of 8.4% and 6.8% ("Griesbach", "unterer Eschwald") and on stands with an infestation three to five times lower (20-30% destruction of the current shoots) in the same general area ("Katzental", "oberer Eschwald") 17.8% and 33.5% parasitism.

Host-preferences: I. maculator is, as are the majority of the members of the Ichneumonid tribe Pimplini, a polyphagous parasite of a number of Microlepidoptera (Tortricidae, Yponomeutidae, Tineidae, Gelechiidae, etc.), Macrolepidoptera (Geometridae, Psychidae, Noctuidae, etc.) and sometimes also an important hyperparasite, attacking Ichneumonids, Braconids and Tachinids (ZWOLFER, 1957). About 2/3 of the host records given by THOMPSON (1957) refer to Microlepidoptera and 1/3 to Tortricids. Among host species with a regular or occasional heavy attack by I. maculator may be mentioned:-

On forest trees: Oak-tortricids such as Tortrix viridana L., Archips xylosteana (L.), etc. (observations by many authors, compare SCHUETTE (1957)), Archips crataegana Hb. (KUDLER & HOCHMUT, 1959), C. murinana on fir, Aphelia viburniana (F.) on Douglas fir (recent observation of BAUSS, 1960). In orchards: Archips rosana (L.)(BAGGIOLINI, 1956). In my own rearings I. maculator has been obtained from the following hosts: Cnephasia virgaureana Tr., C. incertana (Tr.), Tranosema arenicola (Thoms.)(via Cnephasia sp.), Simaethis fabriciana (L.), Olethreutes lacunana (Dup.), Ypsolophus sp. (all on herbaceous plants); A. rosana (on Ribes); T. viridana (on oak). About 45% of the host records in THOMPSON'S catalogue refer to forest insects, 15% to insects in hedges, etc., and 20% to insects in fields, meadows, etc. According to the host spectrum and the biotope preferences of the adults I. maculator is a species showing a wide ecological range in its host selection and a maximum activity in forests*. BAUER (1956) calls it a typical "woodland-form".

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*There remain a number of unsolved questions; for instance the problem of the occurrence of biological races as discussed by HARDY (1938), who did not succeed in breeding I. maculator individuals reared from T. viridana on Plutella maculipennis (Curt.), which in the field, however, is constantly parasitized by an "I. maculator".

In the Vosges we observed considerable parasitism of C. murinana by I. maculator, and on some of the Ichneumonids and Tachinids associated with it a very high hyperparasitism by this species, while the population of T. viridana and A. xylosteana in the same area with which were associated some of the same Ichneumonids (Tranosema arenicola) and Tachinids (Bessa fugax Rond., Blondelia nigripes (Fall.)) was almost completely neglected by I. maculator (ZWOLFER, 1957).

(2) Common species of minor importance

(a) Pimpla turionellae (L.)(Ichneum.-Pimplini)
(P. examinator F.)

Material: 240 individuals

Life history: In all cases observed oviposition took place in host pupae, as in the majority of cases recorded in the literature. However, SCHMITSCHECK (1943) found that P. turionellae attacked and killed larvae of C. murinana. Duration of larval and pupal period: 23-27 days. Soon after emergence (second half of June) the parasites mate and oviposition commences.

Longevity under laboratory conditions: ♂♂ 10-20 days; ♀♀ 40 days or more (AUBERT, 1959: 4 months !). Laboratory rearings on Acleris maccana Tr. and Galleria melonella L. showed that P. turionellae potentially may have three to four further generations, but under the conditions of the observation areas this does not occur. BERRY (1939) mentions six generations per year in New England. BALTENSWEILER (1958), however, records only one generation for the P. turionellae population attacking Z. diniana in the Swiss Alps. The flight period lasts from May to September/October with maxima at May/June and September/October. Several authors (SILVESTRI (1923), SCHWANGART (1918)) have reared overwintering individuals of P. turionellae on hibernating host pupae such as those of Polychrosis botrana Schiff., etc., but fecund females are also able to hibernate (AUBERT, 1959; BERRY, 1939). SEYRIG (1924) found overwintering females of P. turionellae on trees under a cover of moss but only in higher altitudes (800 m. above sea level). SEYRIG supposes a migration of the parasite to its hibernation localities. Ratio of ♀♀

to ♂♂ (1956): Vosges 27:73; Staufen 41:59; Baden-Baden 36:64.

Constancy and abundance: The species is very constantly associated with C. murinana; however, its abundance is relatively low: Vosges (1955) 2.1%, (1956) 1.3%; Staufen (1956) 1.8%; Baden-Baden (1956) 0.7%; Slovakia (1956) 0.1%; FRANZ et al. (1958): Baden-Baden (1956) 0.67%; Gernsbach (1956) 1.44%.

Host-preferences: The host range of P. turionellae is even wider than that of I. maculator, comprising Coleoptera (Curculionids), many families of Macrolepidoptera (Geometrids, Noctuids, Psychids, Pierids, Lymantriids, Lasiocampids, Arctiids, etc.) and Microlepidoptera (Tortricids, Pyralids, Yponomeutids, etc.). Tortricid species (about 15% of the hosts given in THOMPSON'S Parasite Catalogue) do not occupy the dominant position as is the case with I. maculator. Contrasted to I. maculator, P. turionellae also frequently attacks hosts enclosed within parts of the host plant. P. turionellae is sometimes an important parasite of Rhyacionia buoliana (personal observation), Archips piceana (on young Pinus sp., personal observation), Euproctis chrysorrhoea (L.)(AUERSCH, 1955), Zeiraphera diniana on Picea excelsa (PFEFFER, 1930) and on Pinus cembra (BALTENSWEILER, 1958), Yponomeuta evonymellus (L.), Polychrosis botrana, etc. About 35% of the records of host species (THOMPSON) refer to forest insects, 20% to insects of hedges and 45% to insects in agricultural fields and meadows. BAUER (1956) calls P. turionellae a typical "hedge-form" (species with a preference for hedges). Summarizing: P. turionellae may be characterized as a very polyphagous and eurykous

species, which is constantly present (but not dominant) in the types of oak-fir forests investigated here.

(b) Apechthis resinator (Thunb.)(Ichneum.-Pimplini)
(Pimpla quadridentata Thoms.)

Material from C. murinana: 280 individuals

Life history: Females oviposit in the pupae of C. murinana, occasionally also in mature larvae (FRANZ, 1940). The larval and pupal stages are spent within the host and last 22-26 days. Mating takes place just after emergence. As with Pimpla turionellae and I. maculator females may start oviposition a few days after emergence, and thus several generations may possibly occur in a season. Period of flight: May to October/November (BAUER, 1958; personal observations). The mode of hibernation is probably similar to that of P. turionellae. Ratio of ♀♀ to ♂♂: Staufen (1956) 32:68; Baden-Baden (1956) 49:51.

Constancy and abundance: This species has been found in the majority of the rearings of C. murinana, but its abundance was always low: Vosges (1956) 0.3%; Staufen (1956) 1.2%; Baden-Baden (1956) 2.5%; Slovakia (1956) 0.5%. Data of FRANZ et al. (1958): Baden-Baden (1956) 2.4%; Gernsbach (1956) 1.2%; CAPEK et al. (1958): Slovakia (1956) 0.9%.

Host-preferences: In addition to C. murinana this polyphagous parasite has been reared from Lymantria monacha (L.) (TRAEGARDH, 1920 and KOMAREK, 1937); Aporia crataegi (L.), Macrothylacia rubi (L.) (FAHRINGER, 1922); P. histrionana (rarely)(FRANZ, 1952); Adoxophyes orana (F.v.R.)(rarely)(JANSSEN, 1958); A. xylosteana and Tortrix

viridana (numerous authors; CAPEK, 1956; personal observations). The role of A. resinator was not very important in many of the recorded examples. The species seems to be much more stenokous than I. maculator and P. turionellae. The author found it only in forests. The host spectrum and the results of collections of adults (BAUER, 1956) indicate that A. resinator should be considered a typical "woodland-form".

(c) Apechthis rufata (Gmel.)(Ichneum.-Pimplini)

Material from C. murinana: 49 individuals

Life history: A. rufata parasitizes the last larval instar or, more frequently, the pupa of the host. It is potentially able to develop several generations per year. Period of flight: May to October. Ratio of ♀♀ to ♂♂: Baden-Baden (1956) 15:85; Staufen (1956) 20:80. Dr Capek obtained in his rearings in Slovakia only six males and no females (see section IV(B)(5)).

Constancy and abundance: A. rufata occurred in the majority of the rearings of C. murinana, (Table 1), but was, with one exception, of no importance: Staufen (1956) 0.6%; Baden-Baden (1956) 0.3%; Slovakia (CAPEK et al., 1958) 0.2%. FRANZ (1940) reports A. rufata as the second most important pupal parasite in the region of Freiburg/Brg.

Host-preferences: This polyphagous parasite has been reared from several families of Macrolepidoptera, e.g. Geometrids (Ennomos quercinaria (Hfn.)(HUSSON, 1956), Pierids (Aporia crataegi,

(MEYER, 1925), Arctiids, Lymantriids (Lymantria monacha (TRAEGARDH, 1920; KOMAREK, 1937)), Lasiocampids, etc., and of Microlepidoptera, especially Tortricids (A. orana (rarely)(JANSSEN, 1958); A. rosana and A. xylosteana on oak (CAPEK, 1957; personal observations); Z. diniana (rarely)(BALTENSWEILER, 1958); Tortrix viridana (numerous observations)). The species is not only constantly associated with T. viridana but is also one of its most important pupal parasites*. The species is, in view of its host-selection and the biotope - preference of the adults (BAUER, 1956), a typical "woodland-form".

(d) Ephialtes (Scambus) inquisitor (Scop.)(Ichneum.-Ephialtini)

Material reared from C. murinana: 30 specimens

Life history: This species is an endoparasite of the larva of C. murinana which is killed in the sixth instar. According to my observations the parasite larva leaves the host and for pupation spins a thin transparent cocoon (10 mm. x 5 mm.) between the needles of the infested trees. SCHIMITSCHECK (1943), however, reared adults of E. inquisitor from pupae of C. murinana. In the present rearings the pupal period lasted 20-25 days (♀♀) and 16-20 days (♂♂). Mating occurs shortly after emergence. Period of flight (BAUER, 1958): end of April to beginning of August.

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*The A. rufata population in the observation area in the Vosges (1956) parasitized the Tortricid species living on oak (C. xylosteana, T. viridana) but entirely neglected the dense population of C. murinana occurring in exactly the same area on fir. When experimentally transferred to oak, C. murinana pupae were readily and successfully attacked (ZWOLFER & KRAUS, 1957).

Constancy and abundance: In the majority of the observation areas E. inquisitor was reared from C. murinana (Table 1), but its incidence was very low: Vosges (1955, 1956) below 0.5%; Staufen (1956) and Baden-Baden (1956): insignificant.

Host-preferences: This polyphagous species has been recorded from Macrolepidoptera (Lymantriids, Lasiocampids, Pierids, Geometrids, etc.) and from Microlepidoptera (especially Tortricids, Yponomeutids, etc.). In the present work it has been reared from C. murinana, T. viridana, A. xylosteana and (additional observation) Operophtera brumata (L.) and Rhyacionia buoliana. BAUER collected this species mainly on the borders of forests.

(e) Monodontomerus aereus Walk. (Chalc.-Monodontomerinae)

Material reared from C. murinana: 780 specimens

Life history: The female parasitizes host pupa, rarely the full-grown larva of C. murinana. A single host generally yields 3-4 individuals of M. aereus. According to MUESEBECK (1931) there is only one generation per annum and the adults hibernate, prior to emerging, within the dead host pupae (Lymantria dispar, Euproctis chrysorrhoea). When it attacks C. murinana the adult parasites usually leave the host pupa in July or August. Those individuals of M. aereus emerging early may possibly sometimes develop a second generation on pupae of C. murinana (material from the Vosges, 1956). M. aereus may act both as a primary and a secondary parasite. In the observation areas it was mainly the latter, attacking parasites of C. murinana. Of the Cephaloglypta murinanae population 5-9%

were parasitized by M. aereus in the Vosges (1956), and up to 20% at Staufen (1957). I. maculator suffered only 0.5% parasitism in the Vosges (1956) but 4% parasitism at Staufen (1957).

Constancy and abundance: The species has been found associated with C. murinana in most of the observation areas. Its effectiveness (primary parasitism) was usually low: Vosges (1955) below 1%, (1956) 1.7%; Staufen (1956) 1.5%; Baden-Baden (1956) 0.4%; Slovakia (1956) 1.1%. Only once (Staufen 1957) primary parasitism as high as 5.6% was found.

Host-preferences: This very polyphagous parasite has been bred from Diptera (Tachinids, Sarcophagids), Hymenoptera (Ichneumonids, Braconids, Chalcids), Macrolepidoptera (Lasiocampids, Lymantrids, Pierids, etc.) and Microlepidoptera (Tortricids, Yponomeutids, etc.). It is well known as a primary and secondary parasite of Euproctis chrysorrhoea and Lymantria dispar. The majority of its host records refer to forest insects.

(f) Blondelia nigripes (Fall.)(Tachinid.-Blondeliini)

Material reared from C. murinana: 18 specimens

Life history: This ovoviviparous Tachinid attacks the larvae of C. murinana which is actually killed only in the pupal stage. The mature parasite larva then leaves the host and pupates in the soil litter. Emergence takes place in the first half of July. HERTING (1960) mentions a flight period from May to August, and a second generation which overwinters as L_2 within alternate hosts.

Constancy and abundance: This species was reared in the majority of the observation areas but only in very small numbers. In these rearings parasitism by this and other Tachinids never exceeded 0.5%. However, KOLUBAJIV (1934) records the species as a "very frequent" parasite of C. murinana.

Host-preferences: This very polyphagous Tachinid has been reared from many species of Macrolepidoptera (especially Noctuids and Geometrids, but also Sphingids, Lymantriids, Arctiids, etc.). Other hosts occasionally attacked belong to the Microlepidoptera (Tortricids, Yponomeutids) and Tenthredinids (HERTING, 1960). According to this author (HERTING, 1957) this parasite is especially common in pine forests.

(3) Occasional species

In addition to the regularly occurring parasites a large number of species are of accidental occurrence and only a few individuals have been reared from C. murinana. These species are of no economic importance, but they provide a certain theoretical interest when compared with the parasite species of high constancy and abundance. In the following only recent records, mainly species reared by Dr Capek or by the author, are dealt with.

Ichneumonidae

(a) Pimpla instigator (F.)(Pimplini)

Pupal parasite. 3 males reared from C. murinana in central Slovakia (Dr Capek). P. instigator is a very polyphagous parasite of

Macrolepidoptera (Geometrids, Noctuids, Arctiids, Lymantriids, etc.). This rather euryokous species is a frequent parasite of forest pests, well known hosts being Dendrolimus pini (L.), Lymantria monacha, Malacosoma neustria (L.), Euproctis chrysorrhoea, Panolis flammea (Schiff.), Lymantria dispar, Stilpnotia salicis (L.), Dasychira pudibunda (L.), Aporia crataegi. Compared with P. turionellae Microlepidoptera form only a very small part (ca 5% of the species) of the host spectrum of P. instigator.

(b) Itoplectis alternans (Grav.)(Pimplini)

Pupal parasite and hyperparasite. 1 male reared as a secondary through Phytodietus sp. in Central Slovakia (Dr Capek), 1 male bre as a primary from C. murinana in Poland (WIACKOWSKI, 1957). This very polyphagous parasite has been reared from Microlepidoptera (mainly Tortricids, but also Yponomeutids, Gracilariids, Coleophorids, etc.) and, to a lesser extent, from Macrolepidoptera (Geometrids, Lymantriids, etc.). It is well known from Tortricids living on vine (Eupoecilia ambiguella (Hb.), Polychrosis botrana, Sparganothis pilleriana (Schiff.)). It has also been found fairly frequently parasitizing Tenthredinids such as Diprion pini (L.) and Neodiprion sertifer (Geoffr.)(MORRIS et al., 1937). Personal rearing records have been obtained from Acleris boscana (F.)(via Campoplegini sp.) on Ulmus and Gracilaria rufipennella (Hb.) on Acer. I. alternans is a rather euryokous species but it shows, in contrast to the nearly related I. maculator, no preference for hosts in woodland.

(c) Ephialtes calobata (Grav.)(Ephialtini)

Larval parasite. 3 females reared from C. murinana at B. Baden (1936). This polyphagous parasite apparently prefers hosts (Tortricids, Curculionids, etc.) whose larvae are enclosed in parts of the host plants. It is well krown from Balaninus spp. on Quercus, Corylus, etc.

(d) Ephialtes terebrans (Ratz.)(Ephialtini)

Larval parasite. Once reared from C. murinana in the northern Black Forest (BUCHER, 1953). It has been recorded from several Tortricids (e.g. E. ambiguella, Polychrosis botrana).

(e) Phytodietus sp. nr polyzonias (Forst.)(= segmentator Grav.)(Phytodietini)

Larval parasite. Single specimens have been reared from C. murinana in the northern Black Forest (BUCHER, 1953), in the Vosges (BUCHER, 1953)(personal observations 1955 & 1956) and in central Slovakia (CAPEK et al., 1958). This polyphagous species is a typical parasite of Tortricids (e.g. Cnephasia spp., A. rosana). In our observation areas in the Vosges (1955, 1956) and in the southern Black Forest (1957) the species was an important parasite of oak Tortricids (e.g. Tortrix viridana, Pandemis ribeana (Hb.), A. xylosteana, A. crataegana, Ancylis mitterbacheriana (Schiff.)* occurring in the same community as C. murinana, which, in spite of being a physiologically suitable host, was attacked only in exceptional cases.

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*Corresponding observations have been made by Dr Capek (1956) who discusses the host alternation of this parasite.

(f) Glypta sp. nr cicatricosa Ratz. (Glyptini)

Larval parasite. 3 males and 1 female were reared from C. murinana in the Vosges (1955, 1956). This species is probably identical to G. bipunctoria (Thunb.)(sensu CAPEK et al., 1958), one specimen of which was reared in Slovakia from C. murinana. In our observation areas in the Vosges and also in Slovakia Glypta sp. attacked T. viridana on oak. The exceptional parasitism of C. murinana is probably caused by the co-existence of the fir budworm and some oak Tortricids in both of the observation areas.

Two further Glypta sp. (G. crenulata Thoms. and G. fractigena Thoms.), which are perhaps identical to G. nr cicatricosa, have been recorded from C. murinana only in Slovakia (CAPEK et al., 1958).

(g) Chorinaeus longicornis Thoms. (Metopiinae)

Larval parasite which emerges from the host pupa. 3 specimens reared from C. murinana in the Vosges (1955). BUCHER (1953) mentions C. tricarinatus Holmgr. from the same area. The members of the genus Chorinaeus are parasitic on Macro- and Microlepidoptera (especially Yponomeutids). C. longicornis has been bred only from C. murinana pupae found on young firs.

(h) Triclistus globulipes (Desv.)(Metopiinae)

Pupal parasite. A few specimens have been reared from C. murinana in the Vosges (BUCHER, 1953) in Slovakia (CAPEK et al., 1958) and near Baden-Baden (1956). During the present investigations in the Vosges (1955) the parasite was found to be somewhat more abundant (constituting 4% of the pupal parasites). This species had been

recorded from several Microlepidoptera (Tortricids, Olethreutids, Gelechiids). In the present observation areas I. globulipes has only been found on hosts living on young firs.

(i) Tranosema arenicola Thoms. (Campoplegini)

Larval parasite. 2 specimens have been bred from C. murinana in the Vosges (1955, 1956). (Probably some of the "Angitia" spp. mentioned in former parasite lists of C. murinana are identical to I. arenicola). I. arenicola is a typical parasite of Tortricids; it seems often, however, to have been confused with other Campoplegini. Other personal rearing records of the parasite have been obtained from Cnephasia sp. (virgaureana-chrysantheana group) on Ranunculus, from A. rosana on Ribes, Notocelia uddmanniana (L.) on Rubus, and from I. viridana, A. xylosteana and P. ribeana on Quercus. In the observation areas in the Vosges (1956) and near Staufen I. arenicola was one of the most important larval parasites of the oak Tortricids mentioned above, from which in exceptional cases the parasite passed to C. murinana on fir.

(j) Agrypon variitarsum (Wesm.)(Anomalini)

Larval parasite which emerges from the host pupa. 2 specimens were reared from C. murinana in the Vosges (1955) and a few specimens were obtained by BUCHER (1953) at the same locality in 1948; one individual was reared in central Slovakia (Dr Capek). In the literature the parasite is mentioned from Yponomeuta malinellus Z. and from a Noctuid.

In the present observation areas A. variitarsum was only

observed on hosts on young firs.

(k) Blaptocampus nigricornis (Wesm.)(Anomalini)

Parasite emerging from the host pupa. 4 specimens have been bred from C. murinana in the Vosges (1955), 6 specimens at Baden-Baden (1956). In the observation area in the Vosges the parasite was also reared from A. xylosteana (1956) and I. viridana (1957), both on oak. C. murinana was only attacked on young firs.

Braconidae

(l) Meteorus ruficeps (Nees.)(Euphorinae)

Larval parasite. Few specimens have been obtained in the Vosges (BUCHER, 1953); personal material (1955) 1 cocoon. In the northern Black Forest (BUCHER, 1953) and in Slovakia (CAPEK et al., 1958) the species was third in importance among the larval parasites of C. murinana. FRANZ (1952), who published details on the biology and host alternation of this parasite, observed it in eastern Bavaria as most important in attacking P. histrionana and A. piceana on spruce. P. histrionana occurred rather frequently on fir in Slovakia (personal communication Dr Capek, 1956), in forests infested by C. murinana, and it appears probable that M. ruficeps may occasionally pass from these Tortricids to C. murinana, where it does not, however, play an important role.

(m) Eubadizon extensor (L.)(Blacinae)

Larval parasite. A few specimens were bred from C. murinana in the northern Black Forest (BUCHER, 1953), 3 individuals were reared in

central Slovakia (CAPEK et al., 1958). This rather polyphagous species is a typical parasite of Olethreutids and Tortricids. It has been recorded several times from I. viridana and other Tortricids on deciduous trees (A. crataegana, A. rosana). Although it is also mentioned from hosts on coniferous trees (E. nigricarna, Rh. buoliana and Z. rufimitrana) it possibly occurs here only rarely, since it has not been recorded during the present work.

(n) Apanteles ? lineipes (Wesm.)(Microgasterinae)

Larval parasite. This species has been mentioned by BUCHER (1953) as A. dilectus (Hal.)*; it was reared together with another Apanteles sp., probably the typical parasite A. murinanae, from C. murinana in the Vosges and in the northern Black Forest.

Dr Bucher and his assistants bred the same species from Z. rufimitrana (on fir) in southern Bavaria and in Slovakia, where it was "by far the most important parasite" (BUCHER, 1948). From Z. rufimitrana collected in southern Tyrol we found the same species to be second in importance. A. ? lineipes is undoubtedly closely associated with Z. rufimitrana, the redheaded fir budworm, from which host it may occasionally pass to C. murinana.

(o) Ascogaster sp. (Cheloninae)

Larval parasite. One specimen bred from C. murinana in Slovakia (Dr Capek).

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*Material in the reference collection of the European Station, Commonwealth Institute of Biological Control, has been identified by Dr Nixon, Commonwealth Institute of Entomology, as A. ? lineipes (Wesm.)

Chalcidoidea

(p) Amblymerus* subfumatus (Ratz.)(= punctiger Thoms.) (Pteromalinae)

Pupal parasite and hyperparasite. Generally one pupa of C. murinana produces from 4 to 12 individuals. It has been found associated with C. murinana during the present investigations in the Vosges (1955, 1956) and in the northern Black Forest (1956). A total of 281 individuals of A. subfumatus emerged from 36 pupae of C. murinana. However, by dissection it was discovered that A. subfumatus operated mainly as a secondary, feeding on the larvae of the primary parasites. Itoplectis maculator and Phaeogenes maculicornis, and that only about one fourth (Vosges 1956) was primarily parasitic on C. murinana. FRANZ et al. (1958) found 0.7% parasitism by A. subfumatus near Gernsbach and Dr Capek reared 7 females from a single pupa of C. murinana in Slovakia. A. subfumatus is well known from Tenthredinids (Diprionidae). It has been found to be one of the most important primary parasites of Gilpinia polytoma (Htg.)(on spruce), and consequently an attempt was made to establish the species in Canada (MORRIS et al., 1937). The parasite is also recorded from Z. diniana (on larch) in the Tyrol (JAHN, 1948). According to the records available to date this polyphagous parasite seems to prefer hosts on coniferous trees.

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*According to V. ROSEN (1958) the genus Amblymerus Walker 1834 is synonymous with Mesopolobus Westwood 1833.

Tachinidae

(q) Bessa fugax (Rond.)(Exoristini)

Larval parasite which emerges from the host pupa. One specimen was reared from C. murinana in the southern Black Forest (1956), another individual was obtained from the northern Black Forest, where small numbers were also reared by FRANZ et al. (1958). From Slovakia one specimen is mentioned by CAPEK et al (1958). According to Dr Mesnil (personal communication) it is highly probable that B. "selecta Meig." recorded from C. murinana in the Vienna Forest (SCHIMITSCHECK, 1936), in the Black Forest (FRANZ, 1940), in Moravia (SCHIMITSCHECK, 1943), in the Vosges (BUCHER, 1953) and in Poland (WIACKOWSKI, 1957) is identical to B. fugax. In spite of this fairly regular association B. fugax is a very insignificant parasite of C. murinana. This polyphagous tachinid parasitizes many species of Microlepidoptera, mainly Yponomeuta spp. (HERTING, 1960).

(r) Actia maksymovi Mesn. (Siphonini)

Larval parasite. A single specimen was bred from C. murinana in the Vosges (1955). According to HERTING (1960) this tachinid is specialized on host species living on larch (e.g. Sp. lariciana, Z. diniana).

(s) Nemorilla maculosa (Meig.)(Winthemiini)

Larval parasite which emerges from the host pupa. One specimen was reared from C. murinana in the Vosges (1955)(erroneously recorded as N. floralis (Fall.) by ZWOLFER (1956)), another specimen

was bred in the southern Black Forest (1956). Dr Capek reared two individuals in Slovakia. Further records have been published for Moravia (KOLUBAJIV, 1934) and for the Vosges (BUCHER, 1953), but here too the species was of no importance. N. maculosa is a very polyphagous parasite of Microlepidoptera (Pyralids, Tortricids, Gelechiids, etc.), sometimes also attacking Macrolepidoptera (Noctui . etc.). Several generations occur per year (HERTING, 1960).

Sarcophagidae

A "Sarcophagid" sp. was "accidentally" reared from C. murinana by SCHIMITSCHECK (1943) in Moravia. In spite of numerous investigations no further records of Sarcophagids have been obtained of C. murinana.

Mermithidae (roundworms)

Larval parasite. From a few specimens of C. murinana collected in the Vosges (1955) and in the southern Black Forest (1956) a Hexamermis sp. emerged. (Identification by Dr A. Bohm, Erlangen.) Mermithids have also been found by BUCHER (1953) in the Vosges, and by Dr Capek in central Slovakia. In the present observation areas only C. murinana larvae on young firs were attacked by the roundworm.

(4) Hyperparasites

The various types of hyperparasitism in C. murinana and their importance to the host population have already been discussed (ZWOLFER & KRAUS, 1957). Details of the degree of parasitism by the more important hyperparasites have been mentioned in previous sections. In the following only a short summary of recent

observations is given.

Ichneumonids

Itoplectis maculator (F.)(primary and secondary parasite).

Hosts: Tachinid sp. (? Blondelia nigripes)(Vosges 1956); Cephaloglypta murinanae (Vosges 1955, 1956; Staufen 1956, 1957; Baden-Baden 1956; Slovakia, CAPEK et al., 1958); Glypta sp. (Vosges 1956); Tranosema arenicola (Vosges 1956); Meteorus sp. (Vosges 1956).

Itoplectis alternans (Grav.)(not yet found primarily on C. murinana).

Hosts: Cephaloglypta murinanae (Slovakia, CAPEK et al., 1958).

Gelis instabilis (Foerst.)(secondary parasite).

Hosts: Cephaloglypta murinanae (Baden-Baden 1956); Apanteles murinanae (Staufen 1956). (G. agilis (Grav.) has been mentioned from C. murinanae in Slovakia (CAPEK et al., 1958).

Hemiteles areator Panz. (secondary parasite).

Host: Apanteles murinanae (Vosges 1955, 1956; Baden-Baden 1956).

Hemiteles albipalpus Thoms. (secondary parasite)

Hosts: Apanteles murinanae (Vosges 1955; Baden-Baden 1956); Tranosema arenicola (Vosges 1956).

Hemiteles longicauda Thoms. (secondary parasite)

Host: Apanteles murinanae (Staufen 1956; Baden-Baden 1956).

Hemiteles sp. nr longicauda Thoms. (secondary parasite)

Host: Apanteles murinanae (Staufen 1956; Baden-Baden 1956).

Thysiotorus thompsoni Kerrich (Leptocryptus aereus Thoms.) (secondary parasite).

Host: Apanteles murinanae (Baden-Baden 1956).

Mesochorus sp. nr vittator (Zett.)(secondary parasite).

Host: ? (Vosges 1955).

Chalcidoidea

Monodontomerus aereus Walk. (primary and secondary parasite).

Hosts: Cephaloglypta murinanae (Vosges 1955, 1956, 1957; Staufen 1956, 1957; Baden-Baden 1957; Slovakia, CAPEK et al., 1958).

Amblymerus subfumatus (Ratz.)(primary and secondary parasite).

Hosts: Apanteles murinanae (Vosges 1955, 1956); Itoplectis maculator, Phaeogenes maculicornis (Vosges 1956).

Dibrachys cavus (Walk.)(secondary parasite).

Hosts: Cephaloglypta murinanae (Baden-Baden 1956); Apanteles murinanae (Staufen 1956).

Sympiesis sp. (secondary parasite).

Hosts: Apanteles murinanae (Staufen 1956).

? Copidosoma flagellare (Dalm.)(secondary parasite).

Hosts: Cephaloglypta murinanae (Baden-Baden 1956).

Note: Additional occasional parasites and hyperparasites are mentioned in the literature. However, in order to avoid records of one parasite species under several names which, owing to the difficult taxonomic status of many groups of parasites, may easily happen when mere literature references are compiled, only those species which have been bred in our own rearings or compared with our own material have been listed in the foregoing sections. The following occasional parasites not mentioned in the previous sections are recorded in the literature:

KOLUBAJIV (1934)(central Moravia): Ephialtes pictipes (Grav.) Perk., Plectiscus subcurvatus Foerst., Horogenes chrysostictus (Gmel.), Anilasta coxalis (Brischke), Holocremnus sordidellus (Holmgr.), Cremastus ornatus Szepl., Herpestomus brunneicornis (Grav.), Habrobracon brevicornis Wesm., Necremnus leucarthros Thoms., Elachertus sp., Chrysocharis sp., Exorista triseta Pand. (?).

SCHIMITSCHECK (1936)(Vienna Forest): Ephialtes stercorator (F.), Glypta resinanae var. nigrina Desv., Cratichneumon varipes (Grav.), Antesis murinanae Fahr., Hemiteles sordipes Grav., Meteorus scutellator Wesm., Pteromalus pini Htg. (?).

FRANZ (1940)(southern Black Forest): Horogenes armillatus (Grav.), Diadromus troglodytes (Grav.), Hemiteles bicolorinus Grav., H. melanogaster Thoms., Apanteles albipennis (Nees.)(?).

SCHIMITSCHECK (1943)(central Moravia): Pimpla murinanae Fahr., Ephialtes brevicornis Perk., Lissonota variabilis Holmgr., Ichneumon leucoceros Grav., Diadromus troglodytes (Grav.), Phaeogenes invisor (Thunb.), Hemiteles melanogaster Thoms., Apanteles albipennis (Nees.)(?), Apanteles impurus (Hal.), Monodontomerus obsoletus Thoms., M. laricis Mayr., Pachyneuron pruni Walk. (?), Amblymerus mediterraneus Mayr., Pteromalus maculiscapus Ratz., P. pini Htg. (?), "Carcelia sp." (according to Herting: Musca-Phaonia sp.), Phryxe nemea (Meig.), "Phorocera assimilis (Fall.)"(according to Herting: Bessa fugax Rond.), Ernestia connivens (Zett.).

BUCHER (1953)(Vosges): Hypsicera femoralis (Geoffr.), Horogenes vestigalis (Ratz.), Pygostolus sticticus (F.), Apanteles ater Ratz., Pseudoperichaeta insidiosa (R.D.);(northern Black Forest): Horogenes

chrysostictus (Gmel.), H. rufipes (Grav.), H. vestigialis (Ratz.), Aoplus pictus (Gmel.), Hemiteles bicolorinus Grav., Apanteles ater Ratz., Elasmus albipennis Thoms.

CAPEK et al. (1958)(central Slovakia): Phytodietus arcuatorius (Thunb.) Horogenes armillatus (Grav.), Herpestomus flavoclypeatus Strobl., Cyclogastrella deplanata Nees, Phryxe sp.

WIACKOWSKI (1957)(Poland): Ephialtes (Iseropus) roborator (F.), Phaeogenes bisignatus (Holmgr.), Glypta flaveolineata (Grav.), Horogenes varians (Brke), Mesochorus giberius (Thunb.).

(B) Discussion of ecological and biological relationships

(1) Constancy and abundance

In Table 2 an effort has been made to summarize the present rearing results from 1955 (Vosges) and 1956 (Vosges, southern and northern Black Forest, Slovakia). For this purpose the parasite species bred from C. murinana were arranged into three groups corresponding to their abundance and constancy.

The first group, comprising the dominant species Apanteles murinanae, Cephaloglypta murinanae, Itoplectis maculator and Phaeogenes maculicornis, far outnumbers, both in total and also in individual rearings, the large number of remaining parasite species (group II and III). The preponderance of this group, or single species of it, within the rich complex of C. murinana has already been recorded for all the investigation areas (KOLUBAJIV, (1934): central Moravia (only for pupal parasites); SCHIMITSCHECK (1936):

Vienna Forest (only for pupal parasites); FRANZ (1940): southern Black Forest; SCHIMITSCHECK (1943): central Moravia; BUCHER (1953): Vosges, northern Black Forest; CAPEK et al. (1958): central Slovakia; FRANZ et al. (1958): northern Black Forest; WIACKOWSKI (1957): Poland).

There are, of course, regional and seasonal modifications in this, and the abundance of Ph. maculicornis is especially variable (Fig. 2). However, according to the observations made to date, it may be stated that during mass outbreaks of C. murinana* only the four species mentioned above have been able to attain an effective parasitism (i.e. to parasitize 10% or more of the host population).

In view of the comprehensive parasite lists of C. murinana—about 100 species have been named in the literature (CAPEK et al., 1958)—it seems worthwhile emphasizing that it is only a small group of these species which occur in any abundance, and that generally all the remaining parasites have only little influence on the host populations.

The second category of parasites includes those species which appear with some constancy in the rearings (Table 1), but are of relatively low abundance (Fig. 2). The constancy of the parasites of C. murinana has already been discussed by SCHIMITSCHECK (1943) who compared the complex of C. murinana with those of other forest

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*It is not yet possible to give data on the parasitism of C. murinana populations in the phase of "endemic density". During this phase the host is extremely rare, and it becomes very difficult to obtain sufficient material for parasite rearings.

pests. SCHIMITSCHECK emphasized the great disparity of the parasite complexes of the same host species from different observation areas and in different years. With regard to the qualitative aspect of the parasite lists given for C. murinana such differences (for instance the disparity between the western (Vosges, Black Forest) and eastern (Moravia, Slovakia) complexes is quite obvious)*. If, however, the quantitative side of the complexes and the importance of the single species is considered, the similarities between the single complexes, rather than their disparities, become more apparent. We find not only a conformity in the dominant parasites but also among many of the species of minor importance. If the degree of parasitism by the regularly occurring parasites (group I and II) is compared with that of the irregular ones the latter appear to be very insignificant.

In this respect the conclusions of McGUGAN & BLAIS (1959) on the constancy of the spruce-budworm parasites are of interest: "The important elements of the spruce budworm parasite complex are obviously quite uniform regardless of the location in North America. However, each area where intensive studies have been made has produced a somewhat different list of parasites that attack the spruce budworm occasionally. Intensive rearings in other localities will undoubtedly produce somewhat different lists including a few new records. However, the characteristic parasites in any outbreak will

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*These differences are caused partly by the use of different rearing methods, or by incorrect identifications, as has been shown by HERTING (1960) for the Tachinids recorded from C. murinana.

will be drawn from the 12 or 15 species noted above." Practically the same, in our opinion, can be said with regard to the parasites of C. murinana where, however, a smaller number of potentially characteristic species is found.

It appears that such a similarity between parasite or predator complexes observed in different areas and different years is of more general occurrence than is suggested by the lists of species published in the literature. During many years of collection by the European Station of the Commonwealth Institute of Biological Control a general close similarity between the predator complexes of Dreyfusia piceae (Ratz.), the silver-fir woolly aphid, was observed in all the localities investigated between the Vosges and eastern Slovakia, i.e. in a region covering three quarters of the west-east extension of the natural distribution area of silver-fir (PSCHORN-WALCHER & ZWOLFER, 1960). Similar data are available for the parasite complex of the winter moth, Operophtera brumata, where collections in Switzerland, Austria, Germany and Sweden indicate a wide regional constancy of the main parasites (PSCHORN-WALCHER, 1960).

Obviously the remarkable regularity in the occurrence of many parasites of C. murinana is not a matter of chance, but must be due to certain ecological and biological factors. One of these is the generally similar character of the different collection areas, which are forests for the most part situated at the edge of the natural distribution area of silver-fir; these forests contain an admixture of deciduous trees, or at any rate such trees, especially oaks, occur in the immediate vicinity. Thus, a relatively rich reservoir

of host plants is available (SCHIMITSCHECK, 1943). Another probable reason for the constancy of some parasite species is the fact that all the rearings made were from host populations in a high density phase. The third reason for this constancy has to be sought in the general ecology and biology of the parasites concerned. A comparative consideration of some of these ecological and biological features will therefore be given.

(2) Host-range and host-preferences

It must be stated at the outset that these two terms are used only in connection with the parasite populations of the present investigation areas. When observations made in these areas were compared with the findings of other students in this field (AUERSCH, BALTENSWEILER, SCHUETTE, et al.; also personal data) obtained with the "same" species but from other hosts (Euproctis chrysorrhoea, Zeiraphera diniana and Tortrix viridana) and from other areas (northern Germany, Swiss High Alps), considerable deviations in the host-preference (I. maculator, A. rufata), the number of generations (P. turionellae) and the host instar attacked (E. inquisitor, P. turionellae, etc.) have been found. It is not yet clear if these deviations are due to the existence of different biological or host-determined races, or if, on the other hand, they are induced by environmental conditions and consequently are of a purely phenotypic nature. Therefore, the statements on the host-range of the parasites observed have been based mainly on present rearing results or observations by Dr Capek which were made in central Slovakia in similar

communities.

There is wide variation in the host-ranges of the single parasite species of C. murinana. These differences are important biological characteristics of each single parasite species, since they may be considered as an expression of their physiological and ecological potential. In relation to the abundance and constancy of parasite species attacking C. murinana five types of combinations between host-range and host-preference may be distinguished. These types are schematically represented in Fig. 3.

Type 1: Species with relative restricted host-range which, at least during mass outbreaks of C. murinana, concentrate on this host.

Here three of the four dominant parasites must be listed: Apanteles murinanae, Cephaloglypta murinanae and Phaeogenes maculicornis. A. murinanae and C. murinanae have been considered in former publications as monophagous species. Further rearings, especially Dr Capek's systematic investigations on the parasites of forest insects, yielded further records of occasional hosts (pp. 16,18).

Phaeogenes maculicornis, a very peculiar species because of the many enormous variations which occur in its abundance, was not bred from other species in the observation areas, but was observed in other regions parasitizing Tortricids on larch (p. 20).

Common features of these three species are: they are only known from Microlepidoptera, especially Tortricids; they

are very stenokous since they seem to be entirely restricted to coniferous forests; they concentrate in the community on C. murinana, if available; they are able to survive with only one generation per year thus being independent of alternate hosts. Furthermore, A. murinanae and C. murinanae are closely adapted to C. murinana in their bionomics.

Type 2: Species with wide host range (i.e. true "polyvalent parasites") concentrating on the C. murinana population when outbreaks occur.

Only the polyphagous and euryokous Itoplectis maculator is of this type. Its host spectrum comprises Macro- and Microlepidoptera, Hymenoptera, Diptera and probably also some Coleoptera, its ecological range includes forests, garden- and field-biotopes. On the whole Tortricids seem to be preferred among the hosts, and woodland among the biotopes. We have reared this species from various hosts infesting forest trees, shrubs, and herbaceous plants (p. 24) but in the observation areas (Vosges, 1956; Staufen, 1957) it clearly preferred C. murinana and was one of its dominant parasites. In areas of mass-outbreaks of C. murinana oak Tortricids such as I. viridana, etc., have been largely neglected, even though in other areas (SCHUETTE, 1957; AUBERT, 1959; BAUER, 1958 and my own observations in 1959 near Stuttgart), they have been observed to be one of the most important hosts of I. macu-

lator (ZWOLFER & KRAUS, 1957). I. maculator is dependent on alternate hosts (p. 23).

Type 3: Species with wide host-range which attack C. murinana quite regularly but do not show a marked preference for it. Pimpla turionellae, Apechthis resinator, Ephialtes inquisitor, Monodontomerus aereus, Blondelia nigripes belong to this type. All these possess a relatively wide host-range in which Tortricids are well represented; they also occupy various biotopes but seem generally to prefer woodland. Most of them are host-alternating. In these aspects they are similar to I. maculator (Type 2); they do not show, however, its peculiar tendency to concentrate on C. murinana and consequently their abundance on this host is relatively low. The marked constancy in which species such as P. turionellae, E. inquisitor, B. nigripes, etc., are represented in the parasite lists of C. murinana is obviously due to the ubiquity of these euryokous species.

Type 4: Ecologically restricted species which concentrate on other hosts* or occupy other ecological niches of the biocoenosis from which they occasionally pass to C. murinana.

The majority of the "occasional parasites" should be included here. Species belonging to this type have been

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*As an example Meteorus ruficeps, Glypta sp. nr bipunctoria and Eubadizon extensor may be mentioned here. The three parasite species are fairly constantly associated with Archips piceana and Parasyndemis histrionana (both living on fir and spruce) from which they accidentally pass to C. murinana (CAPEK, personal communication).

found to be fairly common in the observation areas, but their host-range was largely restricted by preference for certain host-species, host-plants or strata; C. murinana, although a suitable host, is only attacked in exceptional cases because it does not fit into the host-searching scheme of these parasites. These ecologically restricted parasites will be discussed in more detail in the following section.

Type 5: Species with a wide host-range which only accidentally attack C. murinana.

Among the group of "occasional parasites" there are common species of wide geographical distribution and extensive host-range which are obviously able to parasitize C. murinana but, nevertheless, have only accidentally been bred from this host, e.g. Pimpla instigator, Itoplectis alternans, Habrobracon brevicornis, etc. The reasons for the scarcity of these ubiquitous parasites on this host are unknown. It appears that they prefer hosts which either belong to other systematic groups or live in other communities or ecological niches.

(3) Ecological restrictions of the potential host-range

If only physiological host-suitability, accessibility, and general coincidence in space and time governed the interactions between a given host population and the pool of parasites present in a natural community, it could then logically be assumed that in its parasite

list the polyphagous parasite species would be represented proportionately according to their general abundance in the community and their reproductive power. This would lead to the following consequences:

(a) Different host species with an exactly similar coinciding phenology should exhibit a corresponding series of polyphagous parasites in their complexes when they were in the same community.

(b) The parasite fauna of a given host species should vary greatly in different localities, regions and years according to the changing composition of the reservoirs of polyphagous parasites.

The first point has already been discussed in a former paper (ZWOLFER & KRAUS, 1957). Distinct differences were observed between the parasite complex of C. murinana and those of some other phenologically coinciding potential hosts in the same area. Similar data were found during further investigations (p.59) With regard to the second supposition (b) we have already discussed the relative marked constancy of the more important parasites (p. 46).

Both series of facts show that, in addition to the physiological restrictions and limitations through the lack of coincidence in space and time, the qualitative and quantitative host-relationships of parasites are also influenced by a complex of other factors which offer to each species different possibilities with regard to any given host population.

(1) Among the extrinsic factors interaction of certain parasites with other members of the community may play a modifying

role. Thus, Tachinids in the complex of C. murinana are sometimes seriously affected by competition with the more aggressive hymenopterous parasites. The same is true for the two highly specialized larval parasites Cephaloglypta murinanae and Apanteles murinanae which, in addition, suffer considerably from the attack of typical hyperparasites of the biocoenosis such as Hemiteles spp., Gelis sp., Habrocytus sp., and also from that of predacious bugs, etc. (ZWOLFER & KRAUS, 1957).

(2) On the other hand intrinsic phenomena, such as different ecological preferences and modifications in the searching behaviour, affect the parasite adults in different ways and are largely responsible for the different effectiveness of the parasites of C. murinana. Two types of ecological restrictions may be commented on: restriction of the potential host-range by a preference for certain host-plants or groups of host-plants and restriction of the potential host-range by a preference for certain strata or niches within the community.

These ecological or ethological restrictions operate in a twofold manner. They prevent totally or partially a number of polyvalent parasites from attacking C. murinana, which is a potential host, but they favour other polyphagous species leading them to the ecological niche which C. murinana occupies in the community.

(a) Parasite species associated with fir: Here the stenokous principal parasites A. murinanae, C. murinanae and Ph. maculicornis have to be listed first. They have not only been observed

exclusively on fir in the observation areas but have also always been recorded elsewhere solely on fir, or at least in coniferous forests. Particularly striking in this regard is A. murinanae*. In addition to C. murinana this Braconid has been bred (CAPEK) from Z. rufimitrana, A. piceana, P. histrionana (all feeding on the needles of fir), E. nigricana (feeding within the terminal buds of fir) and Epinotia pusillana (mining in needles of fir (PATOCKA, 1960)).

Although generally a very euryokous parasite, I. maculator, in the observation area in the Vosges (Table 3), definitely preferred hosts on fir to those potential hosts occurring on oak in the same area. The constancy and abundance of I. maculator on C. murinana (Fig. 2) suggest that this behaviour is quite normal when C. murinana occurs at higher densities. In oak forests, on the other hand, I. maculator is an important parasite of species like I. viridana (SCHUTTE, 1957; AUBERT, 1959; BAUER, 1956), A. crataegana and other Tortricids (p. 24).

(b) Parasite species associated with oak and other deciduous trees: In Table 4 three parasite species are listed which, in the observation area, definitely preferred Tortricids on oak, only exceptionally attacking C. murinana on fir. In these

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*The stenokous character of Apanteles murinanae is illustrated by recent ecological investigations in Slovakia.' There the degree of parasitism of C. murinana by A. murinanae was found to be closely correlated to the forest type inhabited by C. murinana. It was highest in the fir-beech association (Abieto-Fagetum), i.e. in a community typical for Abies alba and comparatively very low in the beech-oak association (Fageto-Quercetum) where Abies alba has been artificially introduced (CAPEK, personal communication).

observation areas T. arenicola and P. polyzonias* were the principal parasites of A. xylosteana and T. viridana on oak; they have also been bred from a number of other hosts living on shrubs and herbaceous plants. A. rufata is a constant and abundant parasite of T. viridana, but it was not reared from more than 5,000 pupae of C. murinana collected in 1955 and 1956 in the observation area in the Vosges. However, it readily accepted C. murinana as a host in the same locality when these were transferred to oak (ZWOLFER & KRAUS, 1957). As to parasitism by A. rufata in other regions see p. 28. It is also highly probable that the records of Glypta ? cicatricosa** (Vosges 1956) and Phaeogenes invisor (Thunb.) (SCHIMITSCHECK, 1943) from C. murinana have to be considered as occasional cases of a move from the regular hosts on oak to an unusual host on fir.

(c) Parasite species associated with other host plants. It is certain that the occasional attacks on C. murinana by such normally restricted parasites also take place from other complexes of the community. Only two cases will be mentioned: in the Vosges

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*The autumn generation of this parasite may also be found on hosts on oak (Ancylis mitterbacheriana)(CAPEK, 1956; my own personal observations).

**In Slovakia this species has been observed fairly regularly attacking A. piceana and P. histrionana on coniferous trees (CAPEK, personal communication).

(1955) a single specimen of Actia maksymovi* was reared. This is a Tachinid which has never been previously recorded from C. murinana, although it is widespread (Vosges, Switzerland, Slovakia). According to MESNIL (personal communication) and HERTING (1960) this Tachinid is highly specialized on hosts living on larch.

In the northern Black Forest (1956) four specimens of Ephialtes calobata have been bred from C. murinana. Here, too, there are no other records from fir budworm, but it is well known as a parasite of Balaninus spp. and other hosts living in the fruits of oak, hazel, etc.

(d) Parasites with a preference for certain strata. JAYNES (1954) and MILLER (1959) observed in the American species Apanteles fumiferanae (p. 68), which is ecologically closely related to A. murinanae, a clear preference for the top region of the host-tree. It has not as yet been possible to observe similar characteristics in A. murinanae, but preference for the crowns of mature firs was seen in the stenokous and dominant parasites

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*HERTING (1960) indicates the ecological limitations of some members of the Tachinid genus Actia: A. maksymovi has been bred from larch insects; A. nudibasis Stein is a typical parasite of Lepidoptera living on pine; A. pilipennis (Fall.) is specialized on Tortricids infesting deciduous trees or herbaceous plants. Similar limitations occur in three members of the Ichneumonid genus Phaeogenes, which have been bred from various hosts in the observation area in the Vosges: P. maculicornis attacks hosts on conferous trees (fir, larch); P. invisor is well known from hosts living on oak and other deciduous plants; P. nanus Wesm. is completely specialized to search for pupae of Microlepidoptera in the soil litter.

C. murinanae and Ph. maculicornis (pp. 16, 21). The parasite complex of C. murinana collected from young firs, especially those in thickets, was found to be richer in species but of about equal or even lower effectiveness than the complex observed in the crowns of mature trees (ZWOLFER, 1956).

In the course of the present work the following parasite species have been found attacking C. murinana only on younger firs, principally in thickets, but they have not been reared from host material collected in the same area in the crowns of mature firs: Triclistus globulipes, Blaptocampus nigricornis, Agrypon variitarsum, Chorinaeus longicornis, Hexamermis sp. These species occurred only rarely, and are of low constancy. Since many more hosts have been collected in the crowns of old firs than on young trees in thickets the absence of these species from hosts in the crown stratum is evidently due to an ecological (or ethological) limitation, and not to insufficient host material.

(4) Interrelationships between the complex of C. murinana and other hosts of the community.

In addition to C. murinana a large number of other Microlepidoptera occurring in the community have been reared in order to determine the method of host alternation of the polyvoltine pupal parasites of the fir budworm, especially that of the dominant species, I. maculator. Its regular marked abundance on C. murinana and its polyvoltine life-cycle suggests the presence of a rich reservoir of alternate hosts in the given biocoenosis. We failed

however, to locate these alternate hosts in our observation areas, and we cannot give an explanation of how the relatively high population level of I. maculator in the late spring and early summer is maintained. Dr Capek, who is carrying out a long-term research project on the parasites of Lepidoptera in fir forests, did not succeed in breeding I. maculator from alternate hosts in these forests. He concludes that I. maculator migrates from hosts on other host-plants to fir infested by C. murinana (personal communication). Similar statements have been made for I. maculator and some other Pimplini parasitizing T. viridana in oak forests. Here, too, it seems that no hosts for a second generation are available on oak. (VARLEY et al., 1956; SCHUTTE, personal communication).

Migration of Hymenopterous parasites between hosts belonging to different communities obviously does occur, e.g. ALLEN (1945): migration of Macrocentrus ancylivorus Roh. over short distances in orchards; SEYRIG (1926): migration of females of Amblyteles armatorius (Forst.) in summer from the plains to the mountains; SEYRIG (1926): migration of females of P. turionellae to their overwintering sites in higher altitudes; but the whole problem needs further detailed study.

In the observation areas the following hosts have been reared to obtain parasites:

(a) Hosts on silver-fir (Abies alba)

Epinotia nigricana, Zeiraphera rufimitrana. Both rather common. The parasite complex of E. nigricana included Apanteles longicauda (Wesm.)

Lissonota sp. (principal parasite), Omorgus sp., Mesochorus sp.; Z. rufimitrana was parasitized by Horogenes exareolatus (Ratz.) (principal parasite), Lissonota sp., Apanteles ? lineipes (Wesm., A. murinanae, and Phaeogenes nanus Wesm.

With the exception only of A. murinanae, which passed occasionally from C. murinana to Z. rufimitrana, no connections between C. murinana and these two species of hosts were found.

(b) Hosts on oak (Quercus petraea)

Common species were Archips xylosteana, A. crataegana, Pandemis ribeana and Tortrix viridana. Occasionally Aleimma loeflingiana (L.), Archips sorbiana and Epinotia profundana F. were observed. In the autumn only Ancylis mitterbacheriana occurred at a high density. A parasite list for A. xylosteana and T. viridana has already been given by ZWOLFER & KRAUS (1957). During further investigations (Staufen 1957) some additional species such as Monodontomerus aereus, Macrocentrus sp., etc., were bred from these oak Tortricids. Species occurring in the observation areas which were observed to parasitize both C. murinana and one or several of the Tortricids living on oak are: Ephialtes inquisitor, Blaptocampus nigricornis, Itoplectis maculator, Apechthis resinator, A. rufata, Phytodietus ? polyzonias, Tranosema arenicola, Glypta ? cicatricosa, Monodontomerus aereus. All these cannot, however, be considered as examples of host alternation, but must be taken as simultaneous attack, whereby one of the hosts was always definitely preferred.

(c) Hosts on other deciduous trees

Alnus glutinosa: Gracilaria falconipennella (Hb.), unknown Tortricid sp.; Acer montanus: Gracilaria rufipennella (Hb.); Populus tremula: Tachyptilia populella Cl.; Prunus avia: unknown Tortricid sp. The parasites reared from these hosts in the observation areas showed no connection with the complex of C. murinana. Near Zurich, Switzerland, several males of Itoplectis alternans were reared from G. rufipennella.

(d) Hosts on shrubs and dwarf shrubs

Genista tinctoria: unknown Tortricid sp.; Rosa sp.: Notocelia roborana (Tr.), N. uddmanniana (L.); Rubus sp.: N. uddmanniana; Vaccinium myrtillum: unknown Tortricid sp.; Ribes sp.: Archips rosana. Except for Phytodietus polyzonias, Tranosema arenicola and a few specimens of Itoplectis maculator, all emerging from A. rosana, the parasites reared from the above-mentioned hosts did not belong to the complex of C. murinana.

(e) Hosts on herbaceous plants

Hypericum perforatum: Depressaria liturella (Hb.); Urtica dioica: Simaethis fabriciana (L.), Sylepta ruralis Scop.; Teucrium scorodonia: Pandemis heparana, P. cinnamomcana (Tr.); Prenanthes purpurea, Solidago virgaurea, etc.: Cnephasia sp. In the observation area no connection between the parasites of the above mentioned host species and the complex of C. murinana was found. In further rearings (Black Forest, 1959) Itoplectis maculator (S. fabriciana, P. heparana, Cnephasia sp.) Tranosema arenicola

(ex P. heparana, Cnephasia sp.), and Phytodietus ? polyzonias were also bred from hosts on herbaceous plants.

(5) Sex-ratio and host-preference

Data on the sex-ratio of parasites reared from C. murinana have been given in section IV(a). There are differences according to the collection localities and years, but on the average it may be stated that the differences between the numbers of females and males are not very marked in most of the parasite species.

The sex-ratio of the polyphagous Ichneumonid I. maculator was definitely influenced by its host species (Table 5). Only males of I. maculator emerged from small hosts such as puparia of Tachinids, cocoons of Meteorus sp., Tranosema sp., and in laboratory rearings from pupae of Ephestia kuhniella. This phenomenon is well known in in parasitic Hymenoptera, and has recently been studied in detail for some species of Itoplectis and Pimpla (AUBERT, 1959) and for Pimpla turionellae (ARTHUR & WYLIE, 1959). The size of the host species attacked is obviously not the only factor which has some bearing on the parasite progeny, as is shown in the case of parasitism of Cephaloglypta by I. maculator, when, in spite of Cephaloglypta being a smaller host than the C. murinana, there was a higher proportion of females in the emergent progeny. In this connection it seems worth mentioning that the degree of parasitism by I. maculator was generally higher in Cephaloglypta than in the primary host C. murinana (p. 28). This is in accordance with the view of FLANDERS (1930) who states that the spermatheca of a

of a parasite female is more frequently active if oviposition occurs on a preferred host, and that consequently a higher ratio of female progeny results from parasitism on preferred than on unpreferred hosts: I. maculator prefers the primary parasite Cephaloglypta to the primary host C. murinana, as indicated by the different degree of parasitism, and the ratio of females in its progeny is higher on Cephaloglypta than on C. murinana, which both occur in the same site and are attacked by the same parasite population.

FLANDERS (1946) considers the "occurrence of preferred oviposition site" one of the extrinsic factors determining the sex-ratio of hymenopterous parasites (DOUTT, 1959). Present observations on the host-preference and the sex-ratio of Apechthis rufata may be of interest in this respect. It has already been mentioned that the A. rufata population in the observation area in the Vosges (1955, 1956) readily accepted C. murinana pupae transferred to artificial leaf rolls on oak, but that in spite of adequate numbers of rearings no records of A. rufata were obtained from C. murinana on fir. A few specimens of A. rufata were bred from C. murinana in other regions (Table 6) but most of them were males; only few females were obtained in the southern and northern Black Forest (1956). In contrast to this very low ratio of females from A. rufata on hosts on fir were the results of the transfer tests where only females emerged. From oak Tortricids, i.e. normal hosts of A. rufata, females and males emerge in varying numbers, but no extreme preponderance of one of the sexes seems to have been observed (personal observations, information by Dr Capek and Dr Schutte, etc.). Our own material available is

not yet sufficient to decide whether or not C. murinana transferred to oak is preferred to the oak Tortricids (A. xylosteana, T. viridana), but it permits the conclusion that the preferred oviposition site, i.e. oak leaves, exerts an influence on the sex ratio of the progeny of A. rufata.

V. Parasite complex of C. fumiferana

(A) Literature

In the following only those publications are mentioned which deal with parasites of C. fumiferana and which have been reviewed by the author for the present study.

Parasite lists of the spruce budworm have been given by TOTHILL (1922)(New Brunswick); DAVIAULT (1946)(Quebec); BALCH & REEKS (1946)(New Brunswick); WILKES & ANDERSON (1946)(Belleville, Quebec); WILKES, COPPEL & MATHERS (1948)(British Columbia); DOWDEN, CAROLIN & DIRKS (1950)(Adirondacks, New York). For the very closely related Choristoneura pinus on Pinus banksiana parasite records have been published by WALLEY (1953)(Ontario, Manitoba) and DROOZ & BENJAMIN (1956)(Michigan).

Special studies on single parasite species have been undertaken by BROOKS (1945)(Lypha setifacies (West.)); BROWN (1946a)(Apanteles fumiferanae), (1946b)(Glypta fumiferanae); HOUSE (1951)(Pseudosarcophaga affinis (Fall.)); COPPEL (1951)(Phytodietus fumiferanae (Roh.), effects of super-, multi- and hyper-parasitism on its abundance); ARTHUR & COPPEL (1953)(Sarcophaga aldrichi Park.);

MAW & COPPEL (1953)(*Phryxe pecosensis* (Tns.)); MILLER (1953)(parasitism by *Trichogramma minutum* Ril.); COPPEL & MAW (1954a) (*Ceromasia auricaudata* Tns.), (1954b)(*Madremyia saundersii* (Will.)); COPPEL & SMITH (1957)(*Omotoma fumiferanae* (Tot.)).

Other publications deal with techniques, assessment, physiological and ecological relationships: HOUSE & GLADYS TRAER (1948)(techniques involved in the propagation of spruce budworm parasites); MILLER (1955)(assessment of spruce budworm parasites); McGUGAN (1955)(physiological host-parasite relationships); JAYNES (1954)(influence of the host-site (different crown heights) on *Glypta* and *Apanteles*); BLAIS (1958)(influence of abnormal climatic conditions on some parasites); COPPEL (1946)(overwintering habits of some spruce budworm parasites); WEBB (1956), WEBB, McDONALD & CAMERON (1958)(influence of insecticides); WILKES (1946)(differences in the regional distribution of some species in North America).

Studies on the influence of parasites on the population dynamics of the hosts have been made by MORRIS, MILLER, GREENBANK & MOTT (1956)(population dynamics of larval parasites); MILLER (1959)(population dynamics of *Apanteles fumiferanae*); JAYNES & DROOZ (1953)(general population trends of several budworm parasites). Recently, McGUGAN & BLAIS (1959) published an interesting study on the constancy, relative abundance and population trends of spruce budworm parasites in north-western Ontario.

(B) Present investigations

The following list has been compiled mainly from WILKES & ANDERSON (1946)(observations in Ontario, 1946, and Quebec, 1946); WILKES, COPPEL & MATHERS (1948)(observations in British Columbia 1943-47); DOWDEN, CAROLIN & DIRKS (1950)(observations in the Adirondacks, 1946-48); McGUGAN & BLAIS (1959)(observations in north-western Ontario). The degree of constancy was estimated on the basis of the number of records of the parasite species concerned from the host C. fumiferana. Some figures of the relative abundance have been given in order to demonstrate the potential importance of the more common species. An effort has been made to assess the value of all the common and regularly occurring parasites, and also of some of the occasional ones, which have been mentioned in recent literature.

(1) Egg parasites

Trichogramma minutum Ril. Rather constant but generally of low controlling value. Occasional observations of greater abundance: Adirondacks (1947) 13% parasitism; New Brunswick (1948-49) parasitism locally reaching 40% (MILLER, 1953); Ontario (1946) 12% parasitism. HEWITT (cited by WILKES et al., 1946) found in 1911 over 75% of eggs parasitized by Trichogramma.

(2) Parasites attacking hibernating larvae.

Glypta fumiferanae (Vier.). Constantly associated with C. fumiferanae (McGUGAN & BLAIS (1959): occurrence rating 0.95), abundance varying in relation to host density. From British Columbia (1943-47) mentioned as the most important parasite species

(average abundance: 5.18%). In Ontario (1946) and Quebec (1946) not exceeding 2%. In the Adirondacks (1946) up to 10%.

Horogenes cacoeciae (Vier.). Of rather low constancy (McGUGAN & BLAIS (1959): occurrence rating 0.05) and, in general, not very effective, in the Adirondacks locally reaching 10% (1946). In New Brunswick (1945) very effective at low host density (BALCH & REEKS, 1946). According to MILLER (1959) common during endemic periods of the host population.

Apanteles fumiferanae Vier. Constantly associated with C. fumiferanae (McGUGAN & BLAIS (1959): occurrence rating 0.98), abundance varying in relation to the host density. MILLER (1959): in New Brunswick with low host density parasitism is generally below 5%, while at higher host densities it increases to 20% or even more. Average parasitism in British Columbia (1943-47), in Ontario (1946) and Quebec (1946) not exceeding 2%. In the Adirondacks (1946-48) varying between 4 and 10%.

Apanteles spp. Occasionally small numbers of Apanteles spp. other than fumiferanae have been reared from the spruce budworm: A. petrovae Wly., A. polychrosidis Vier., Apanteles sp.

(3) Parasites attacking small larvae in buds, etc.

Dicladocerus sp. In the Adirondacks (1946-48) fairly effective against small larvae of C. fumiferana feeding in buds and on staminate flowers. There were also occasional specimens of Elachertus cacoeciae How. and Tetrastichus sp. Nothing can be said of the general constancy of these three Chalcid species.

(4) Parasites usually attacking medium-sized or full-grown larvae.

Scambus hispae (Harr), Sc. alboricta (Cress.). Both these species are of rather low constancy and, generally, negligible in numbers.

Phytodietus fumiferanae Rohw. In British Columbia (1943-47) fairly constantly associated with C. fumiferana, second of the parasites in importance with an average parasitism of 3.83%. In eastern Canada not present but, according to WILKES & ANDERSON (1946). successfully introduced into Ontario.

P. vulgaris Cress. (= P. annulatus (Prov.)). Occasional parasite. Only mentioned from the Adirondacks (1946-48); of negligible importance.

Bracon sp. nr politiventris (Cush.). Of fairly low constancy and negligible importance. In the Adirondacks it parasitized, together with Scambus alboricta, 1% of the host larvae.

Oncophanes atriceps (Ashm.). Occasional parasite. Mentioned from the Adirondacks, of negligible importance.

Clinocentrus sp. Occasional parasite. Mentioned from the Adirondacks, in 1947 locally effecting 3% parasitism.

Eubadizon sp. Occasional parasite. Mentioned from the Adirondacks, of negligible importance.

Meteorus trachynotus Vier. Fairly constantly associated with C. fumiferanae (McGUGAN & BLAIS (1959): occurrence rating 0.95), varying widely in its abundance in relation to the host density. Apparently increasing in numbers with a decline of the host

(DOWDEN et al., 1950; JAYNES & DROOZ, 1953). In the Adirondacks reaching, temporarily, an average parasitism of 11% (1948).

M. hyphantriae Ril. Occasionally reared in small numbers in British Columbia (1948) and in the Adirondacks.

Actia* (Gymnophthalma) interrupta (Curr.). Fairly constantly associated with C. fumiferana; numbers in British Columbia (1943-47) very low, on the average not exceeding 0.02%; in the Adirondacks (1948) of some importance in light infestations.

Winthemia amoena (Meig.)* (Omotoma fumiferanae (Tot.)). Of high constancy (McGUGAN & BLAIS (1959): occurrence rating 0.77), but of varying abundance. In British Columbia (1943-47) most important of the dipterous parasites of C. fumiferana with an average parasitism of 2.41% but locally reaching 14%. Also mentioned as the most important Tachinid parasite of the spruce budworm in Colorado (COPPEL & SMITH, 1957). In Ontario (1946) and Quebec (1946) not exceeding 2%. In the Adirondacks (1946-48) relatively important.

Nemorilla maculosa (Meig.)* (Nemorilla pyste (Wlk.), N. floralis (Fall.)). Perhaps only one species. Fairly constant, but, in general, relatively rare.

Phryxe* (Madremyia) saundersii (Wilk.). Fairly constantly associated with C. fumiferanae, but generally relatively rare,

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*I am much indebted to Professor L.P. Mesnil for his comments on the systematic status of the Tachinid parasites of C. fumiferana. In the ensuing list names marked with an asterisk refer to the generic conception of MESNIL (1944).

uncommon (Adirondacks, 1946-48); in British Columbia (1943-47) the average parasitism was about 0.65%. Only from Colorado a higher parasitism (14-20% from both larval and pupal collections) has been recorded (COPPEL & MAW, 1954).

Phryxe pecosensis (Tns.). Of very high constancy and sometimes of importance. Average parasitism in British Columbia (1943-47): 1.10%. In the Adirondacks (1946-48) parasitism varying between 6-18% (emergence from larvae) and 3-6% (emergence from pupae). Decreasing in abundance with decreasing host infestations (JAYNES & DROOZ, 1953).

Pseudoperichaeta* (Phorocera) erecta (Coq.). Only mentioned from British Columbia (1943-47); of rather high constancy there but not abundant (average parasitism: 0.33%).

Eumea* (Aplomyia) caesar (Ald.). Rather constantly associated with C. fumiferana (McGUGAN & BLAIS (1959): occurrence rating 0.52), abundance varying, very low (average below 0.5%) in British Columbia (1943-47); in Ontario (1946) 2.1%; in Quebec (1946) 3.6%; in the Adirondacks (1946-48) varying between 4-17% (emergence from larvae) and 1-15% (emergence from pupae).

Clemelis* (Phorocera) incrassata (Smith.). In British Columbia of high constancy and of some importance; average parasitism during 1943-48 1.10%. Apparently not present in eastern Canada but transferred there (WILKES, 1947).

Ceromasia auricaudata Tns. In British Columbia of high constancy and fairly abundant; according to COPPEL & MAW (1954) fourth and fifth parasite in importance, sometimes causing a

a parasitism of 13% (average in 1943-47 2.06%). Transferred from western to eastern Canada for release against C. fumiferana.

Erynnia** (Phorocera) tortricis (Coq.). Occasional parasite of low constancy and negligible importance. Mentioned from British Columbia (1946, 1947) and from the Adirondacks.

Lypha setifacies (West.). Of high constancy (McGUGAN & BLAIS (1959): occurrence rating 0.75) and sometimes very abundant. Average degree of parasitism in British Columbia (1943-47) 1.32%. In the Adirondacks (1948) varying between 2-18%. "Important parasite" in Ontario and Quebec (BROOKS, 1945). Increasing in importance with decreasing infestation (JAYNES & DROOZ, 1953).

(5) Parasites attacking full-grown larvae or pupae.

Pimpla pedalis Cress. Of rather low constancy and negligible importance. Mentioned from British Columbia and eastern Canada (Ontario (1946): 1 specimen from 255 host pupae).

Apechthis ontario (Cress.). Very constantly associated with C. fumiferanae (McGUGAN & BLAIS (1959): occurrence rating 0.80) and sometimes abundant. In British Columbia (1943-47) most important hymenopterous pupal parasite with an average parasitism of 1.95%; similarly in the Adirondacks (1943-47) where the species was responsible for 11-20% reduction of the late pupal stage. In Ontario (1946) and Quebec (1946), however, distinctly less abundant than the pupal parasite Itoplectis conquisitor. According to

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**According to MESNIL this species belongs to a new genus which is closely related to Nemorilla.

JAYNES & DROOZ (1953) decreasing with decreasing density of C. fumiferana.

Itoplectis conquisitor (Say). Of high constancy (McGUGAN & BLAIS (1959): occurrence rating 0.75) and occasionally fairly important. Negligible in British Columbia (1943-47), in eastern Canada rather common (Ontario (1946): 26 specimens from 255 host pupae; Quebec (1946): 13 specimens from 45 host pupae). In the Adirondacks (1946-48) parasitism varied between 3 and 8%. Decreasing in abundance with decreasing host density (JAYNES & DROOZ, 1953).

I. obesus Cush. Of rather low constancy and not abundant; in British Columbia (1943-47) giving an average parasitism of 0.32%.

Phaeogenes hariolus (Cress.). Fairly constantly associated with C. fumiferana (McGUGAN & BLAIS (1959): occurrence rating 0.73), occasionally of some importance. Average parasitism in British Columbia (1943-47) 0.7%. Up to 4% parasitism mentioned from the Adirondacks in 1948. Increasing in abundance with decreasing host population (JAYNES & DROOZ, 1953).

Exochus sp. Occasional parasite of low constancy and generally of negligible importance. Fairly abundant, however, during light infestations in New Brunswick (DOWDEN et al., 1950). According to MILLER (1959) common during endemic periods of C. fumiferana.

Monodontomerus montivagus Ashm., Monodontomerus ? subobsoletus Gahan. Occasional parasites of low constancy and negligible importance. Reared in small numbers in British Columbia in 1944.

Amblymerus verditer (Nort.). Rather constantly associated with C. fumiferana (McGUGAN & BLAIS (1959): occurrence rating 0.42), but

mostly operating as a secondary parasite. Primary parasitism very uncommon.

Pseudoscarcophaga affinis (Fall.). Not very constantly associated with C. fumiferana, but of some importance (average parasitism: 1.63%) in British Columbia (1943-47).

(6) Hyperparasites

(See WILKES, COPPEL & MATHERS (1948) and DOWDEN et al. (1950)).

Itoplectis obesus Cush. Occasionally hyperparasitic on Phytodietus.

Scambus hispae (Harr.) Primary and secondary parasite (ex Glypta and Phytodietus).

Gelis tenellus (Say). Hyperparasite.

Eucorus ? thoracicus (Cress.). Hyperparasite, ex Phytodietus.

Mesochorus sp. Hyperparasite ex Glypta, Phytodietus, Apanteles.

Spilochalcis sp. Hyperparasite ex Glypta and Apanteles.

Monodontomerus montivagus Ashm., M. ? subobsoletus Gahan. Probably both primary and secondary parasites.

Habrocytus phycidis Ashm. Possibly a secondary parasite.

Amblymerus verditer (Nort.). Probably both primary and secondary (ex Phytodietus, Itoplectis conquisitor, Ephialtes ontario). In 1946 in the Adirondacks these pupal parasites suffered 4-36% secondary parasitism by A. verditer and Nasonia torticis (Brues), but practically no secondary parasitism was observed in 1948.

(7) Parasites of the Jack-pine budworm, C. pinus.

DROOZ & BENJAMIN (1956) reared the following parasites from C. pinus on Pinus banksiana in Michigan:- larval parasites: Glypta fumiferanae, Apanteles fumiferanae, Actia interrupta, Lypha setifacies, Phryxe pecosensis. Pupal parasites: Itoplectis conquisitor, Apechthis ontario Cress., Ephialtes hispae, Phaeogenes hariolus, Exochus sp., Amblymerus verditer, Habrocytus sp., Pseudosarcophaga affinis. Egg parasite: Trichogramma minutum.

VI. Similarities and differences between the parasites of C. murinana and C. fumiferana

(A) General

In the following an attempt is made to compare the individual members of the parasite complexes of the fir and spruce budworms. Such a comparison meets with certain difficulties: the area from which C. fumiferana and its parasites are known (from eastern to western North America) extends over about five times as great a distance as does the area of C. murinana and its known parasites (from eastern France to Poland). It is probably mainly a consequence of this wide distribution area of the spruce budworm that the occurrence of some of its parasites is regionally limited (e.g. Phytodietus fumiferanae), while others are of different importance in different areas. The complex of C. murinana, on the other hand, shows a greater uniformity.

The studies on C. fumiferana and its parasites, which cover

epidemic and endemic phases of the host population, are much more complete than the investigations on the host and parasite complex of the European fir budworm which are in general restricted to periods of high host density.

These factors limit the scope of this comparative study. A number of facts, on the other hand, appear to be quite favourable to the comparison: both complexes exhibit a considerable uniformity, especially in their dominant and common elements; they are, moreover, of about equal size with regard to numbers of species and show a similar structure. The degree of importance of the single parasite species is also comparable if the potential effectiveness of the parasites is taken into consideration.

(B) Comparison of the complexes of the fir and spruce budworms.

In their studies on the parasitism of the spruce budworm in the Adirondacks and in Maine DOWDEN et al. (1950) and JAYNES & DROOZ (1953) give figures for the percentage of various host stages killed by parasites, which might perhaps be used for a general comparison of the effectiveness of both budworm complexes, if only parasitism during periods of higher host density is considered (Adirondacks 1946; Maine 1949-50; Vosges 1955-57; southern Black Forest 1956-57).

The figures given in Table 7 can only be considered as a general indication of the effectiveness of the individual parasite groups. They show, however, important and constant differences between the complexes of C. murinana and C. fumiferana: the

occurrence of egg parasites and the important role of parasites, mainly Tachinids, in killing mature larvae in the spruce budworm and their absence or insignificance in the fir budworm. No generalization is possible with regard to the Chalcid parasites of young host larvae, since these have been observed only in a few cases in North America and are not known hitherto from the fir budworm in Europe.

It has already been mentioned that many parasite species of the fir and spruce budworms belong to common genera or tribes. As a basis for the following comparison a synopsis of these corresponding parasite species is given in Table 8. Species marked with an asterisk are potentially dominant parasites while names in parentheses indicate only occasional parasites.

(C) Comparison of equivalent parasite species

(1) Trichogramma minutum

To date no egg parasites of C. murinana have been found in spite of intensive search undertaken on several occasions. In the present work rearings of ample egg material from the Vosges (1958) and the southern Black Forest (1959) gave no evidence of the occurrence of Trichogramma sp. These observations are in sharp contrast to the situation with C. fumiferana where egg parasites occur frequently and sometimes in large numbers (p. 67).

(2) Cephaloglypta murinanae and Glypta fumiferanae

(a) Systematic position. BUCHER (1948) stated that in the opinion of several specialists "Glypta murinanae BAUER" is

sufficiently different from other known members of the genus to warrant placing it in a new genus. This was carried out by OBRTEL (1956), who separated his "Cephaloglypta excavata n.sp." (= C. murinanae BAUER) from the genus Glypta "from which it differs mainly by the occipital impression of the head and by impressions on tergites 2 and 3 forming distinct triangular fields". In spite of the close general relationship of both genera, Cephaloglypta murinanae occupies a rather isolated position within the Glypta group, its most characteristic feature being the peculiar structure of the occiput (Fig. 4).

G. fumiferanae, on the other hand, belongs to that species group of the genus Glypta which is characterized by the possession of a prominent concave tubercle on the head above the antennae (Fig. 4). Several authors, including Viereck, who in 1912 described this budworm parasite under the name Conoblasta fumiferanae, considered this group to be a distinct genus (Conoblasta, FOERSTER, 1868).

Among the European species Glypta (Conoblasta) extincta (Rtzb.), a parasite of Archips rosana, is morphologically (structure of the head, general sculpture and coloration) very close to G. fumiferanae. Also Glypta (Conoblasta) ceratites (Grav.), a common parasite of Tortricids (personal records from Olethreutes lacunana) is similar to G. fumiferanae.

Within the compass of the Glypta group the European C. murinanae and the North American G. fumiferanae are clearly separated by the following characters: (1) structure of the head (Fig. 4);

(2) differences in the proportion of, and the sculpture on, the abdominal tergites; (3) different lengths of the antennae in the males, and of the ovipositor sheets in the females; (4) sculpture of the propodeum; (5) punctures on the thorax; (6) proportions of the tarsal segments; (7) pigmentation of the head, thorax, abdomen, antennae and legs. While in G. fumiferanae both the sexes are rather similar, C. murinanae shows a marked sexual dichromism (colour of head and legs).

If C. murinanae and G. fumiferanae are compared with other Glypta species it is obvious that there is no direct phylogenetical relationship between them, such as is assumed for their host species C. murinana and C. fumiferana. These parasites cannot be traced back to a common ancestor parasitic on the ancestors of C. murinana and C. fumiferana, but they must have originated from two different lines of Glypta species which, independently of each other, attacked the various Choristoneura species preceding C. murinana and C. fumiferana*

Whilst nothing can be stated here as to the position of the rather isolated C. murinanae, it is easy to connect G. fumiferanae with the morphologically very similar European members of the Conoblasta group such as G. extincta and G. ceratites, both of which are rather polyphagous parasites of Tortricids. G. fumiferanae

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*A third line of Glypta which is potentially able to attack this host complex may be seen in Glypta cicatricosa (p. 35) which exhibits neither a direct relationship with Cephaloglypta nor with the Conoblasta group.

may be considered as a biologically and ecologically specialized descendant of this group.

(b) Hosts and biology. MUESEBECK et al. (1951, 1958) record C. fumiferana and C. pinus (on Pinus banksiana) as the main hosts of Glypta fumiferanae, and in addition the Lymantriid Hemerocampa pseudotsugata McD. on Pseudotsuga taxifolia and the Tortricid Acleris variana (Fern.) on Tsuga canadensis and Abies lasiocarpa. Thus its host range is restricted to a very small number of species living on coniferous trees, just as also occurs with the European Cephaloglypta (p. 16). G. fumiferanae appears to have a distinct preference for C. fumiferana and its sibling species C. pinus, to which hosts its univoltine life-cycle (parasitism of hibernating larvae, overwintering as a first instar larva in the host) is adapted in the same way as that of the European Cephaloglypta to the fir budworm (p. 15). Both parasites are very constantly associated with their hosts and their effectiveness is generally similar, i.e. relatively low (pp. 16, 68).

C. murinanae and G. fumiferanae exhibit a striking similarity in their host-ranges and host-preferences, their highly specialized biology, their constancy and importance, but they are morphologically distinctly different, and cannot be regarded as a phylogenetic pair of species. Their corresponding biology must, therefore, be construed as a result of adaptive convergence caused by specialization on corresponding host species.

(3) Iranosema arenicola and Horogenes cacoeciae

(a) Systematic position. It was only possible to compare one female of H. cacoeciae with Iranosema arenicola and Horogenes chrysosticta which, probably erroneously, had been recorded from C. murinana. H. cacoeciae differs from H. chrysosticta (wing venation, sculpture of the propodeum) but in its general morphology, its sculpture and pigmentation, and in the shape and colour of its cocoon, it is very similar to I. arenicola (females), slight differences* between these species having only been found in the colour of the coxae, the sculpture of the first abdominal segment, and in the venation of the forewing. Although placed in different genera both species seem to be rather closely related.

(b) Hosts and biology. H. cacoeciae was described from specimens reared in British Columbia from A. rosana. It is, moreover, an irregular and usually not very effective parasite of C. fumiferana (p. 68). This univoltine species parasitizes the hibernating host larvae and overwinters in the first larval instar. The European I. arenicola is an important parasite of A. rosana (p. 36) but has only in a few cases been bred from the fir budworm.

I. arenicola and H. cacoeciae are similar in their morphology and host-range, but they differ in that H. cacoeciae seems to show a certain tendency to attack the spruce budworm also in the

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*Only one specimen of H. cacoeciae was available; it remains in doubt therefore whether these differences are normal or whether they merely represent individual variation which is considerable in Iranosema arenicola.

absence of other hosts, while T. arenicola is a very insignificant parasite of the fir budworm and has only been bred from this host when it was common as a parasite of A. rosana and other oak Tortricids in the vicinity.

(4) Apanteles murinanae, A. fumiferanae and other Apanteles spp.

(a) Systematic position. To group the European A. murinanae, A. ? lineipes, the North American A. fumiferanae, A. petrovae and similar species, we have used the propodeum and the first two abdominal tergites (Figs. 5 & 6). A. murinanae and A. petrovae may be grouped together by a close similarity in the structure and sculpture of these parts (Fig. 5). Both species are, moreover, morphologically very similar. They differ in the colour of the tibiae, tarsi and mouth parts. A. dioryctriae, a species very nearly related to A. murinanae, must also be included in this group.

A. fumiferanae and A. ? lineipes have in common their striking difference from the "murinanae-group". Although showing distinct differences in the sculpture of the propodeum, the sculpture and shape of the second tergite, and in the colour of the legs, they are morphologically more closely related to each other than to the A. murinanae-A. dioryctriae-A. petrovae group*.

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*This grouping of Apanteles spp. cannot pretend, of course, to lead to systematic subdivisions, since only a few species out of several hundreds in the genus have been examined. The object is merely to assess the morphological relationships of the Apanteles parasites of the fir and spruce budworms.

(b) Hosts and biology. A. fumiferanae has been bred from Acleris variana (Fern.)(on Tsuga canadensis and Abies lasiocarpa) and from Dioryctria abietella (D.& S.)(in cones of Abies spp., Pinus spp., etc.), but its main hosts are C. fumiferana and C. pinus. This univoltine parasite, which oviposits in the hibernating host larva and overwinters in the first larval instar, is highly specialized on the spruce budworm. It is constantly associated with this host and sometimes reaches considerable abundance (p. 68). A. murinanae is in its ecology, host range, host preference, constancy and importance, very comparable with A. fumiferanae, but this ecological and biological similarity is, as in the case of the Glypta parasites of the fir and spruce budworms, not parallelled by a morphological relationship. With Apanteles too an independent specialization and convergent evolution of species originating from different polygenetic lines has to be assumed.

In this regard it is of special interest to compare the hosts of A. dioryctriae and A. petrovae with those of A. murinanae. A. dioryctriae was described by WILKINSON (1938), from specimens bred from Dioryctria peverimhoffi de Joann, mining in the young cones of Cedrus atlantica in Morocco. It is, according to WILKINSON'S description and further information from Mr Nixon (Commonwealth Institute of Entomology) the closest species to A. murinanae among the known Apanteles species. A. petrovae, which is obviously related to A. dioryctriae and A. murinanae, has been recorded in North America from Petrova albicapitana (Busck)

(mining in young twigs of Pinus) and is also an accidental parasite of the spruce budworm (MILLER, 1959) and the Jack-pine budworm. If, however, the host-range of the European A. murinana, with its complete restriction to Microlepidoptera living in the twig-and-shoot-region of Abies alba, is taken into consideration, the conclusion seems to be justified that these geographically widely separated, but morphologically and ecologically similar, species may derive from a common group of ancestors connected with hosts on coniferous trees.

It is a peculiar fact that the principal Apanteles parasite of the American spruce budworm did not originate from this "murinanae-group", especially since a member of this group (A. petrovae) is not only present in the communities concerned but also proves to be a potential parasite of C. fumiferana. In spite of this ecological and physiological preadaptation to the spruce budworm the ancestors of A. petrovae did not become specialized on this host in the same way as did the ancestors of the related A. murinanae on the fir budworm. This niche was eventually filled by A. fumiferanae, a member of quite a different group. Consequently A. murinanae and A. fumiferanae have to be considered as analogous, not as homologous, species. There seems even to be an analogy in the host range: A. fumiferanae is able to attack both Choristoneura and Dioryctria and thus becomes equivalent to the species pair A. murinanae-A. dioryctriae in the old world. In the author's opinion this indicates the occurrence of corresponding parasitilogical trends in the two

separated Apanteles-groups.

A. ? lineipes (p. 38), a typical parasite of Z. rufimitrana, the European red-headed fir budworm, also on rare occasions parasitizes C. murinana which lives in the same habitat as E. rufimitrana. The species is ecologically specialized in a similar way to A. murinanae and A. fumiferanae, and it shows some morphological resemblance to the latter species. If a real phylogenetic relationship existed between the American A. fumiferanae and the European A. ? lineipes, an analogous situation to that in A. murinanae-A. petrovae could be assumed. Anyway, it seems obvious that the Apanteles parasites of the fir and spruce budworms have been derived from separate ancestor groups which apparently had in common a certain association with hosts on coniferous trees, and that the two main parasites are examples of an adaptive ecological and biological convergence (Fig. 7).

(5) Dicladocerus sp., Tetrastichus sp., Elachertus sp.

Species of these genera have been observed attacking the smaller larvae of C. fumiferana in vegetative buds and staminate flowers. Dicladocerus sp., the most important parasite of this group, seems to parasitize mainly host larvae feeding on pollen, and its differantial abundance may be in part connected with a varying production of staminate flowers (DOWDEN et al., 1950). No equivalent parasite group has been observed in the fir budworm. The somewhat different behaviour of the young larvae of the European fir budworm, which are only able to penetrate opening

buds, and also the lower production of staminate flowers by the European silver fir (FRANZ, 1957), may be one of the reasons for this difference in the parasite complex of C. murinana and C. fumiferana.

(6) Ephialtes (Scambus) inquisitor and S. hispae.

(a) Systematic position. It was possible to compare the majority of European Ephialtes species with S. hispae, and it was found that among their vast number E. inquisitor, E. buolianae (Hart.) and E. nucum (Ratz.) are morphologically closely related to S. hispae. The female of S. hispae keys out in SCHMIEDEKNECHT to E. inquisitor, but differs from this European species in the darker colour of the stigma, a somewhat different colour of the abdomen, and a slightly different colour pattern on the hind tarsi and tibiae. In the pigmentation of the abdomen and legs S. hispae corresponds to E. (S.) buolianae and E. (S.) nucum, from which species, however, it differs in other characters (length of antennae, etc.). The male of S. hispae closely resembles that of E. inquisitor but the colour of the stigma is also darker. S. hispae and E. inquisitor are obviously related species.

(b) Hosts. The wide host range of S. hispae includes some Macrolepidoptera (Lymantriids) and many Microlepidoptera (especially Tortricids, but also Coleophorids, Gelechiids, Pyraustids), thus corresponding to the host range of E. inquisitor (p. 30). Another similarity between these two parasites may be

seen in the fact that both their host lists contain many forest species. S. hispae, for instance, has been reared in North America from the imported Rh. buoliana, while E. inquisitor is a rather important native enemy of the same species in Europe. Both parasites have more than one generation a year. In the complexes of Choristoneura spp. both the Ephialtes species are of negligible importance, but the European E. inquisitor occurs more regularly than S. hispae.

Thus, E. inquisitor and S. hispae are systematically closely related parasite species with equivalent host-range and corresponding relationships to the fir and spruce budworms.

(7) Phytodietus ? polyzonias and Ph. fumiferanae

(a) Systematic position. Specimens of Ph. ? polyzonias from the present investigations show a considerable variability in the distribution of the yellow pigment, rendering a comparison with other species somewhat difficult. In their general appearance, sculpture and coloration Ph. ? polyzonias and Ph. fumiferanae are very similar to each other; the two species differ, however, in both sexes in the proportions of the abdominal tergites and in the colour of the hind femora. Their cocoons may be distinguished very easily, that of Ph. ? polyzonias being yellowish and transparent with an opaque band around the centre, whilst that of Ph. fumiferanae is totally opaque and of a greyish paper-like appearance.

(b) Hosts and biology. Ph. fumiferanae is recorded only from C. fumiferana. The species seems to be specialized on this host; it has a univoltine life-cycle, oviposits in the late larva of the host and overwinters as a mature larva in its silken cocoon. Ph. fumiferanae was found to be one of the most important budworm parasites in British Columbia (p. 69). Ph. ? polyzonias, on the other hand, is rather polyphagous (p. 34), at least two-brooded, and attacks the fir budworm only exceptionally.

Ph. ? polyzonias and Ph. fumiferanae are consequently, in spite of a certain morphological resemblance, very different in their host range, biology, and in the position they occupy in the complexes of the fir and spruce budworm.

(8) Meteorus ruficeps and M. trachynotus

(a) Systematic position. M. ruficeps and M. trachynotus are rather similar in their general appearance, but they differ in the sculpture of the propodeum, in the shape and sculpture of the first abdominal segment, and in the colour of the thorax, abdomen, hind tibiae and tarsi.

(b) Hosts and biology. Meteorus trachynotus has been recorded from several Tortricids, including Acleris variana (on Pseudotsuga, Abies, etc.) and Archips argyrospila (Wlk.)(on deciduous trees). It is well known as a parasite of Grapholitha molesta (Busck). The species is fairly regularly parasitic on C. fumiferana but generally not very abundant (p. 70). It completes its development in the full-grown host larva which

continues to live for several days after the parasite larva emerges. M. trachynotus requires an alternate host for hibernation (DOWDEN et al., 1950). M. ruficeps (p. 37) resembles M. trachynotus in its biology (its host larva also survives for several days after the emergence of the parasite larva), its host alternation (FRANZ, 1952) and, to a certain extent, its host-preference; but it is only an occasional parasite of the fir budworm.

M. ruficeps and M. trachynotus are fairly similar in their morphology, biology and host-range, but differ in their regularity and abundance in the complexes of fir and spruce budworm.

(9) The Tachinid parasites

I have to thank Professor L.P. Mesnil for his comments on all the Tachinid species mentioned.

Blondelia nigripes is a fairly regular parasite of C. murinana but is never common. No corresponding species is known from C. fumiferana.

Actia maksymovi and A. (Gymnophthalma) interrupta. The latter species is a fairly regular but not very important parasite of the spruce budworm. A. maksymovi, the only European member of the genus reared to date from the fir budworm, has only been found once, probably as the result of an accidental attack.

Winthemia amoena (Omotoma fumiferanae) is a very regular and sometimes fairly important budworm parasite in North America. According to REINHARD & TOWNSEND (MESNIL, personal communication) C. fumiferanae is identical to the European W. amoena, which, however, is considered to be a specific parasite of Panolis flammea (HERTING, 1960). No Winthemia species has been bred from C. murinana.

Nemorilla maculosa. The American Nemorilla "pyste", a fairly regular but not very abundant parasite of C. fumiferanae, is considered by MESNIL (personal communication) to be identical to the European N. maculosa, which has been reared occasionally, and only in very small numbers, from C. murinana. Thus N. maculosa must be considered to be a holarctic species which parasitizes both the fir and the spruce budworms. It appears noteworthy that, as seems normally the case with Tachinid parasites of Choristoneura spp., the American host species is more regularly attacked, and to a higher degree, than the European host.

Phryxe (Nadremyia) saundersii and Ph. pecosensis are fairly regular and, sometimes, important parasites of C. fumiferanae. The European Ph. vulgaris (Fall.), a very polyphagous parasite of Macrolepidoptera, is very closely related to Ph. pecosensis. The only Phryxe sp. which had been bred from C. murinana is Ph. nemea (SCHIMITSCHECK, 1943: 1 specimen). Pseudoperichaeta (Phorocera) erecta is a comparatively regular and sometimes important parasite of C. fumiferana. It is very closely related to the European P. insidiosa R.D. which was once reared in small numbers from C. murinana (BUCHER, 1953).

Eumea (Aplomyia) caesar is a very regular and sometimes important parasite of C. fumiferana. This Tachinid is very closely related to the European E. mitis, a parasite of Microlepidoptera, especially Tortricids. No Eumea species has been reared from C. murinana.

Clemelis (Phorocera) incrassata, a regular and important parasite of C. fumiferana in British Columbia, is closely related to Pseudoperichaeta.

Ceromasia auricaudata, also a very constant and often very abundant parasite of C. fumiferana, is not represented by a corresponding European species in the complex of C. murinana.

"Erynnia" (Phorocera) tortricis, an occasional and uncommon parasite of C. fumiferana belongs to a new genus which is very close to Nemorilla.

Lypha setifacies is regularly and sometimes very commonly associated with C. fumiferana. The closely related European L. dubia (Fall.), an important parasite of Operaphtera brumata and some forest Tortricids, has not as yet been bred from C. murinana.

The Tachinid complexes of the fir and spruce budworms show remarkable differences. Reared from C. murinana there is only one species of regular occurrence (Blondelia nigripes), and this is uncommon, together with about five occasional species of negligible importance, whilst four regular and often abundant species (Eumea caesar, Lypha setifacies, Winthemia amoena, Phryxe pecosensis) and six to seven fairly regular species of minor importance are known from C. fumiferana. The European species are of negligible importance as control factors of C. murinana, only about 0.5-1% of the total parasitism in Dr Capek's and the author's rearings was due to Tachinids. In the complex of C. fumiferana, however, Tachinids are responsible for about 30-40% or more of the total effect of parasites. Corresponding species in the parasite complexes

of the fir and spruce budworms are much scarcer among the Tachinids than among the hymenopterous parasites. Only the genera Actia, Nemorilla, Pseudoperichaeta and Phryxe are represented (but not equally) in both the complexes. Members of other genera have hitherto only been recorded from one of the two budworms.

The quantitative and qualitative disparity of the Tachinid parasites of C. murinana and C. fumiferana is a very interesting problem which needs further study. According to MESNIL (personal communication) these differences may be partially explained by the somewhat different phenology of each of the hosts. Development of C. murinana larvae takes place relatively early in the season (April to the beginning of June) and thus a number of potential Tachinid parasites are certainly prevented from attacking this host by a time factor. The larval period of the American budworm occurs generally about three to five weeks later than that of C. murinana and it falls in a period of relatively higher temperature (Fig. 1). Owing to this there is perhaps a better general synchronization between the budworm and potential Tachinid parasites in the community.

(10) Pimpla turionellae and P. pedalis

(a) Morphological relationships. P. turionellae is distinctly different from P. pedalis (colour of the hairs on the head and thorax, punctures on the thorax, pleurites of the abdomen, colour of the legs). Among the European Pimpla species P. pedalis is morphologically similar to those of the "instigator" group, especially to P. arctica (Zett.), which differs only in the colour

of the coxae and trochanters.

(b) Hosts. The host-range of P. pedalis consists preponderantly of Macrolepidoptera such as Lymantriids, Lasiocampids, Arctiids, and only a few Tortricids. In this respect too P. pedalis is rather similar to P. arctica, and different from P. turionellae, which parasitizes Macro- and Microlepidoptera to about the same extent. Many of the hosts of P. pedalis are typical forest insects (Lambdina fiscellaria (Guen.), Malacosoma americana (F.), Gilpinia polytoma and others) and it is probably a certain ecological preference for forests which causes the occasional attack by P. pedalis on C. fumiferana.

P. turionellae, on the other hand, is a very regular parasite of the European fir budworm (p. 26). It has successfully been established in Canada against the imported European pine-shoot moth, but has as yet not been reported as a parasite of the spruce budworm.

P. turionellae and P. pedalis belong to different groups within the genus Pimpla; they also differ in their host-range and in their position in the complexes of the two budworms.

(11) Apechthis resinator, A. rufata, A. ontario

(a) Morphological relationships. The American A. ontario is strikingly similar to A. resinator among the European Apechthis species, correspondences being visible in the sculpture, the shape of the epipleura, the basal lobes of the foreclaws, the coloration and other characters. It is even difficult to separate the European and the American species since only graded differences (colour of

the hind femora, tibiae and tarsi in females, colour of the antennae in males) have been found. The European A. rufata is quite similar to A. resinator and A. ontario, but it may easily be distinguished from these by the simple hind claws (females), the punctures on the sixth and seventh tergites, and by the pigmentation.

(b) Hosts and biology. The host-range of A. ontario comprises typical forest insects such as Ellopia sp., Argyrotaenia murinana (Fern.) and Dioryctria reniculella (Grote) and is thus similar to that of A. resinator. The European and American Apechthis species are normally dependent on alternate hosts, but A. ontario has once been observed overwintering as a mature larva in a pupal case of C. fumiferana (COPPEL, 1946). A. ontario and A. resinator are both very regular parasites of the budworms but the first species is a dominant and sometimes most abundant pupal parasite of C. fumiferana, while A. resinator generally only ranges third or fourth in importance among the pupal parasites of C. murinana. A. rufata occurs less regularly than A. resinator and is usually scarce.

A. ontario and A. resinator are morphologically very closely related species with corresponding host-ranges and ecological preferences. Within the budworm complexes A. resinator is inferior to the important A. ontario.

(12) Itoplectis maculator, I. alternans, I. obesus, I. conquisitor.

(a) Morphological relationships. The European I. maculator and I. alternans are rather similar species which may be separated

by means of the punctures and hairs on the thorax, and the colour of the hind trochanters. The American I. obesus keys down to I. alternans but differs from this species in the sculpture of the propodeum and the colour of the antennae and hind tibiae. I. conquisitor, on the other hand, shows a certain resemblance to I. maculator, but the two species may be distinguished by the colour of the legs, the colour of the abdominal tergites, and in the female, by the colour of the antennae. When these species are compared with other members of the genus Itoplectis their close relation becomes obvious.

(b) Hosts and biology. I. conquisitor is a very polyphagous parasite of Macro- and Microlepidoptera (mainly Tortricids) and is also able to hyperparasitize Ichneumonids and Braconids. Forest insects constitute a large part of its host list. The species is dependent on alternate hosts and may overwinter either as an adult or in an immature form (DOWDEN et al., 1950).

I. maculator is very similar to I. conquisitor in its host-range, its preference for forest insects, and its biology. Furthermore, both these species occupy a similar dominant position among the pupal parasites of the fir and spruce budworms. The control value of I. maculator is, however, reduced by its strong tendency to attack Cephalcglypta murinanae in addition to the primary host, while secondary parasitism by I. conquisitor appears not to be common in the complex of C. fumiferana.

The American I. obesus is abundant west of the Continental Divide. According to MUESEBECK et al. (1951) it is a typical

parasite of coniferous forests attacking Tortricids, Gelechiids, Geometrids, etc.

In the complex of the spruce budworm it is generally not very common. Only in the western parts of North America (British Columbia) was the species reared from C. fumiferana more frequently than I. conquisitor.

I. alternans, is merely an accidental parasite of C. murinana in spite of its euroky and its wide host-range.

I. maculator and I. conquisitor are equivalent parasite species which correspond in their morphology, biology, host-range, ecological preference and in their importance as parasites of the fir and spruce budworms. I. obesus is a species which apparently replaces I. conquisitor in western North America and it shows a greater similarity to I. alternans which, however, differs from the three other Itoplectis species in that its attack on the budworm is only accidental.

(13) Phaeogenes maculicornis and Ph. hariolus

(a) Morphological relationships. Ph. maculicornis and Ph. hariolus are morphologically very similar and exhibit a number of common characters which indicate their close relationship within the genus Phaeogenes (general appearance, sculpture of the propodeum, tubercles on the hind coxae of the females, etc.). The two species may be separated by slight differences in the colour of their mandibles, palpi and last abdominal tergites (females), and in the colour of the scapus and scutellum (males). The

specimens of Ph. maculicornis reared from C. murinana show a wide colour variation, and some males and females (described as "var. gigas ab. brunnea" by FAHRINGER (SCHIMITSCHECK, 1943)) are distinguishable from Ph. hariolus only with difficulty.

(b) Hosts and biology. The host-range of Ph. hariolus is, as in Ph. maculicornis, relatively narrow and apparently ecologically limited to insects on coniferous trees (Acleris variana, Neodiprion tsugae Middl., C. fumiferana and C. pinus). Both species are able to survive with only one generation a year and both hibernate in the adult stage (COPPEL, 1946). In the complexes of the fir and spruce budworms Ph. maculicornis and Ph. hariolus are fairly regularly observed but with great variations in their abundance. The European species is sometimes first in importance among the pupal parasites of C. murinana; Ph. hariolus, however, apparently is more effective only in declining host populations (JAYNES & DROOZ, 1953).

Ph. maculicornis and Ph. hariolus may be considered as systematically closely related species characterized by corresponding host-ranges, bionomics and ecological preferences, and playing a similar role in the parasite complexes of the fir and spruce budworms, only differing in that Ph. maculicornis may become more abundant than Ph. hariolus.

(14) Occasional Ichneumonid parasites of little importance.

Mention must be made, in addition to the corresponding parasite species of the two complexes, to those for which hitherto no equivalent partner has been found in the complex of the other host.

These are the usually unimportant Exochus sp. from the spruce budworm and the ecologically limited Chorinaeus longicornis, Triclistus globulipes, Agrypon variitarsum and Blaptocampus nigricornis (p.59), all occasional parasites of the fir budworm.

(15) The Chalcid parasites of the genera Monodontomerus and Amblymerus.

No comparison can be made between the European Monodontomerus aereus on C. murinana and the American species M. montivagus and M. ? subobsoletus which occasionally parasitize C. fumiferana. It appears that the American species are less frequent in the budworm complex than the European M. aereus, and it is also uncertain whether the two American species show the same well developed tendency to hyperparasitize other budworm parasites as is seen in M. aereus.

Although successfully introduced into North America the European species has not as yet been recorded from C. fumiferana.

The European Amblymerus (Mesopolobus) subfumatus, an occasional parasite of the fir budworm, and the American A. verditer, a fairly regular species in the complex of C. fumiferana, have to a certain extent been confused and considered as belonging to the same species. According to VON ROSEN (1958) they differ only very slightly from each other (punctures, structure of the antennae), but are easily separated from all the remaining species of the large genus Amblymerus by a common peculiarity in the sculpture of the thorax. VON ROSEN even considers the possibility of erecting a new genus for these two Pteromalids.

Both the species are parasites of forest Lepidoptera and sawflies (Diprion spp.) and both may act as secondary parasites. Hyperparasitism by these species is much more important than primary parasitism in the complexes of the European and American budworms: A. subfumatus has been found attacking Apanteles murinanae, Itoplectis maculator and Phaeogenes maculicornis. A. verditer has been bred from Phytodietus fumiferanae, Itoplectis conquisitor and Ephialtes ontario. The primary parasitism on C. murinana (p. 43) and C. fumiferana (DOWDEN et al., 1950) is generally practically negligible.

Thus A. subfumatus and A. verditer are very closely related parasites with corresponding hosts and a similar position in the budworm complexes.

(16) The Sarcophagids

Pseudosarcophaga affinis is not very regularly associated with C. fumiferana but it has sometimes been recorded as a parasite of a certain importance (HOUSE, 1947). From C. murinana an undetermined Sarcophagid species has been bred only once and in small numbers (SCHMITSCHECK, 1943). Obviously, Sarcophagids show the same unequal representation in the complexes of the fir and spruce budworm as do the Tachinids (p. 91).

(D) Summary

In the following a short synoptic summary of the preceding comparisons is given. The parasite species are classified according to their morphological relationships and their role in the complexes of the two budworms. Category 3 (morphologically related species) represents the intermediate position between the distinctly separate and the closely related species.

(1) Parasites without corresponding forms on the other host: The Chalcids, Trichogramma minutum, Dicladocerus sp., Elachertus cacoeciae and Tetrastichus sp.; the Ichneumonid, Exochus sp.; and the Tachinids, Eumea caesar, Ceromasia auricaudata, Lypha setifacies, Winthemia amoena, Clemelis incrassata and Erynnia tortricis, all only on C. fumiferana, the Tachinids, Blondelia nigripes and Bessa fugax and the Ichneumonids, Chorinaeus longicornis, Triclistus globulipes, Agrypon variitarsum and Blaptocampus nigricornis, all only on C. murinana.

(2) Corresponding parasite species which belong to distinctly different groups of the same genera or tribes:-

(a) Stenokous, biologically highly specialized, dominant budworm parasites: Cephaloglypta murinanae - Glypta fumiferanae; Apanteles murinanae - A. fumiferanae.

(b) Unspecialized species of minor or very little importance: Apanteles ? lineipes - A. petrovae (apparently stenokous, and with rather restricted host-range); Pimpla turionellae - P. pedalis (rather polyphagous, "woodland" species).

(3) Corresponding parasite species which are morphologically similar:

(a) With similar host-range and similar position in the budworm complexes: Itoplectis maculator - I. conquisitor, I. obesus (very polyphagous, multivoltine, sometimes with a tendency towards secondary parasitism, dominant pupal parasites in the budworm complexes); Ephialtes (Scambus) inquisitor - S. hispae (polyphagous, rather eurokous, but apparently with a certain preference for forests, rather unimportant parasites of budworm larvae).

(b) With unequal position in the budworm complexes: Apechthis rufata - A. ontario; Tranosema arenicola - Horogenes cacoeciae; Phytodietus ? polyzonias - Ph. fumiferanae; Meteorus ruficeps - M. trachynotus; Actia maksymovi - A. interrupta; Phryxe nemea - Ph. pecosensis (all of some or great importance with regard to C. fumiferana, but of minor or negligible importance in respect to C. murinana).

(4) Corresponding species which are identical or morphologically very closely related (i.e . more similar to each other than to other members of the genus). With similar host-range and similar ecological preferences:

(a) Similar position in the budworm complexes: Phaeogenes maculicornis - Ph. hariolus (very stenokous "woodland" forms, important pupal parasites of both the budworms); Amblymerus subfumatus - A. verditer (negligible as primary parasites, sometimes important hyperparasites in each of the budworm complexes).

(b) Unequal position in the budworm complexes: Apechthis resinator - A. ontario (polyphagous "woodland" forms,

multivoltine pupal parasites, important in the C. fumiferana complex, of minor importance in that of C. murinana); Nemorilla maculosa - N. maculosa (pyste); Pseudoperichaeta erecta - P. insidiosa (of some importance with C. fumiferana, negligible with C. murinana).

VII. Discussion and conclusions

(A) General

Choristoneura spp. possess, like all other holometabolic insects, several biologically and ecologically differentiated stages, which are attacked by a number of different types of parasites. Host species such as these offer to entomophagous insects a system of diversified opportunities for oviposition and larval development, providing what, in analogy with the ecological niches of a habitat, may be considered as a complex of "parasitological niches".

These niches will be naturally occupied by parasites, even by specialized forms, if the host species is native in its community. A poor utilization of these niches and lack of more specialized parasites, on the other hand, may be regarded as a plausible argument for a rather recent connection between the host and its community (as with introduced insect pests and insect pests which have transferred their attentions to another often introduced crop), especially if rich and diversified parasite complexes occur in related host species. As an example may be cited the European parasite complex of the larch sawfly, Pristiphora erichsonii (Hart.),

including relatively specialized forms such as Mesoleius tenthredinis (Morley), Hyalurgus lucidus (Meigen), etc., and the absence of regular parasites of the Canadian populations of P. erichsonii. This lack of a native Canadian parasite complex may be taken as an indication that P. erichsonii has been introduced into North America (PSCHORN-WALCHER, 1961). The rich parasite complexes of the fir and spruce budworms, however, and the occurrence of specialized forms such as Apanteles spp., Glypta spp. and Phytodietus fumiferanae indicate a native status of both the host insects and an ancient association between the hosts and their communities.

The concept that host species represent complexes of well characterized niches for the development of various animal parasites has proved to be a promising one in the field of general comparative parasitology, where it has been used in connection with problems of host phylogeny, biogeography, general evolution and speciation of parasites. For examples we refer to BAER (1952), CAMERON (1956) and OSCHE (1957). Practically all these comparative studies concern parasitic groups such as Nematodes, Cestodes, Anoplura, Mallophaga, etc., but there has been little consideration of the vast field of entomophagous parasites. In an endeavour to apply this principle to this latter group also an attempt has been made in the following pages to discuss some biogeographic, evolutionary and ecological aspects of the two budworm parasite complexes from the point of view of comparative parasitology. First, however, the special status of hymenopterous and dipterous insect "parasites" must be compared with that of the parasite groups mentioned above, i.e. with the "true

parasites" in the parasitological sense.

(B) Parasitoids and parasites

The parasitic Hymenoptera and Diptera which have been dealt with in this study are designated "parasitoids" by some authors. According to DOUTT (1959) "they are recognized as being different from parasites because: (a) the development of an individual destroys its host; (b) the host is usually of the same taxonomic class, i.e. Insecta; (c) in comparison with their hosts they are of relatively large size; (d) they are parasitic as larvae only, the adults being free-living forms; (e) they do not exhibit heterocism; (f) as a parameter in population dynamics their action resembles that of predators more than that of true parasites". It should be pointed out that none of the characteristics cited can be considered as an absolute criterion applicable to all parasitoids and to no true parasites. The theoretical differentiation between parasitoids and parasites seems, nevertheless, to be justified, although the former term has not gained widespread usage*.

In the present study three differences between parasites sensu stricto (especially the typical parasites of Vertebrates such as Cestodes, Trematodes, etc.) and parasitoids seem to be of special interest:

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*Following the majority of authors we have generally not used the term "parasitoid" in the present study. We speak of parasitoids only where it was thought advisable to emphasize the contrast to parasites sensu stricto.

(1) Although several "true parasites" such as some parasitic Copepods, Gordiids, etc., are known to possess free-living adult stages, the vast majority occur either with free-living larval stages and parasitic adults (parasitic snails, many parasitic Copepods, fleas, etc.) or with both larvae and adults parasitic (many parasitic Nematodes, Trematodes, Acanthocephalans, Cestodes, parasitic mites, biting lice, true lice, etc.). Consequently, the morphological, physiological and ecological characteristics of these forms are essentially adapted to parasitism (BAER, 1952). The life-cycle of parasitoids, however, is divided into two phases: a parasitic phase (larvae) with typical morphological, physiological and behaviouristic adaptations to parasitism, and a free-living phase (adults) with corresponding adaptations to free life in the surrounding biocoenosis. In the latter phase the adult parasitoid exhibits very many characters of its morphology (occasional occurrence of semantic colour patterns, etc.), diversified behaviour (feeding, mating, migrations, overwintering, etc.), and ecological limitations and preferences, which are not primarily connected with parasitism, but with the free life in the community. Thus, generally speaking, the parasitic period within the host and the free-living period within the biocoenosis may be considered as of about equal biological rank.

The dominant role of the host and its ecology, ethology, and phylogeny in the evolution of "true parasites" is well known (BAER, 1952)(OSCHE, 1957). In parasitoids, however, where one stage is distinctly adapted to and influenced by free life in the

community, the possible bearing of the latter on the evolution of the groups and species has also to be considered in addition to any effects of the host.

(2) BAER (1952) emphasizes the considerable differences in types of host specificity in "true parasites" and parasitoids. In the former group random distribution of progeny frequently occurs and host specificity is in general primarily of an ecological nature (e.g. in many parasitic Nematodes, Trematodes, Mallophaga, etc.), whilst in most parasitoids any host specificity of the parasitic larval phase is caused primarily by the psychic pattern of the adult, which actively chooses the hosts for its offspring. There are exceptions such as some Tachinids with microtype eggs, Trigonalids, Eucharids, etc., where eggs are distributed on the hostplants, etc., but in general parasitoids are characterized by some form of host searching on the part of the adult female and by direct oviposition into or on the host. Consequently, relatively slight changes and deviations in the behaviour and psychism of the adults may exert a considerable influence on the host range and on the evolution of a parasitoid species.

(3) Food supply is almost always plentiful for the parasitic stages of "true parasites". There does not appear "to be any evidence of competition for survival" (BAER, 1952). This lack of competition is considered to be favourable for the survival of a large proportion of mutations and may thus become an evolutionary factor (BAER, 1952).

On the other hand, in the parasitic phase of hymenopterous and dipterous parasitoids food supply is often limited and competition in or on an individual host is a phenomenon of general occurrence. This competition is well known in several forms of multiple parasitism and hyperparasitism (both terms sensu SWEETMAN, 1936). In the first case an "individual host is attacked more than once by one or more species of parasites, the broods developing simultaneously". If two species attack different stages of the host an indirect competition in the amount of available food may occur. If the same stage is parasitized the two forms come into direct competition and ordinarily only one survives. In the case of hyperparasitism one parasite species attacks another parasite species, the female being attracted to the primary host only secondarily or incidentally. In many cases hyperparasitism derives from multiple parasitism and may hence be considered as a final result of an original competition for survival*.

The possible adverse influence of competition on the evolution of physiologically restricted "monophagous" parasitoids must be taken into particular consideration when these are compared with monophagous forms of "true parasites".

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*This is well illustrated by Itoplectis maculator which generally acts as a primary. In the complex of C. murinana it meets with another primary, Cephaloglypta murinanae, and develops a strong tendency to hyperparasitize the latter species.

(C) Lack of specific phylogenetic parallelism in the Choristoneura parasites.

A well-known phenomenon in parasites such as biting lice, sucking lice, parasitic Nematodes and others, which has even been the basis for the formulation of "parasitological rules" is the systematic correlation between related host and parasite groups and species. These correlations are brought about by parallel evolution connecting higher systematic categories of hosts and parasites (for instance the subfamily Ischnopsyllinae (Siphonaptera) being exclusively parasitic on bats) as well as lower categories (the genus Paleopsylla on shrews and moles) or even related species (the parasitic beetle Platypsyllus castoris Rits. on the European and American beaver). Such a "phylogenetic specificity" (BAER) is not restricted to parasites; it has, for instance, also been seen in some commensal Nematodes associated with bark-inhabiting beetles (RUEHM, 1955).

Correlations between higher categories of hosts and parasites also frequently occur in entomophagous parasitoids. For example the Aphidiinae are associated with aphids. Many genera among the budworm parasites mainly or exclusively attack hosts belonging to Tortricids and related families, or to the suborder Microlepidoptera: Phytodietus spp. are external larval parasites of small Lepidoptera, mainly Tortricids and related families; Phaeogenes spp. are internal pupal parasites of Lepidoptera; Glypta spp. are internal larval parasites of Lepidoptera, mainly Microlepidoptera; Apanteles spp. are likewise internal larval parasites of Lepidoptera, etc. All these parasite genera show a physiological and biological adaptation to host species belonging to the same systematic unit, and this must

be considered as an indication of an ancient association between both groups of partners.

The question arises as to whether, in insect parasitoids, phylogenetic parallelism occurs also at a specific level. It was one of the aims of the present study to examine this question in connection with the specialized budworm parasite species of the genera Apanteles and Glypta, which might be supposed theoretically to be preadapted to a phylogenetic specificity. We have already pointed out (pp. 78, 82) that such a phylogenetic parallelism does not exist in the budworm complexes studied, and that it is replaced by an ecological parallelism which has apparently influenced the evolution of the Apanteles and Glypta species concerned in a convergent manner. Neither can the close systematic relationship between budworm parasites such as Phaeogenes maculicornis and Ph. hariolus be considered as a result of specific parasitological "parallel evolution", since here the connection with the community (and not with a single host species) must be regarded as the dominant factor.

It is probably that the host restriction and specialization of the ancestors of Apanteles murinanae, A. fumiferanae, Cephalolglypta murinanae, Glypta fumiferanae and Phytodietus fumiferanae took place only after the topographic separation of the ancestral hosts had already occurred, since otherwise it might be assumed that at least one pair of the specialized parasites should have a direct common origin. Another reason for presuming such a comparatively recent date of specialization may be seen in the fact that all the

species concerned are not strictly monophagous. If now the situation in the Apanteles spp. and the Glyptini concerned is compared with that of a monophagous "true parasite" such as the Platypsyllus castoris mentioned above, the specificity of which is apparently very much older* than that of the above mentioned specialized Apanteles and Glypta species, a difference between the "true parasite" Platypsyllus and these parasitoid species becomes apparent. The strict and long-established monophagy does not apparently involve any particular hazard for Platypsyllus, as is demonstrated by its survival on geographically isolated hosts. An absolute monophagy of these parasitoid species, on the other hand, reduces in the long run their chances of survival because of competition with other parasitoids, because of a more complicated and therefore more vulnerable method of attacking hosts, and probably also because of greater variations in the host density. Owing to the lack of complete intimate connection between the parasitoids and their insect hosts, this risk may be compensated for by the fact that even specialized parasitoids generally appear to possess the ability to parasitize additional host species in the community occasionally.

The lack of phylogenetic specificity in the highly adapted Apanteles and Glypta parasitoids of Choristoneura spp. does not, of course, exclude the possible occurrence of such a phenomenon

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*BAER (1952): "Since this parasite is closely associated with its host, it appears probable that it had already become adapted to them in Tertiary times when both the European and the American beavers lived on the same continent".

in other parasitoid species. It does, however, demonstrate again, in the author's opinion, the special situation of insect parasitoids with their twofold relationship to host and community.

(D) Biogeographical aspect

It has already been stated that the parasite complexes of related but topographically separated hosts may be used too in the formulation of biogeographical conclusions. At present, where the extent of the knowledge of the fauna differs on the different continents, a zoogeographical analysis of well-investigated parasite complexes of corresponding host species will offer an additional tool for students in biogeography since, in this way, relatively limited and well-known equivalent ecological units may be compared. A broad comparative study of entomophagous parasite complexes would also be of general interest as a basis for biological control work, the aim of which may be considered as an improvement in the relative distribution patterns of insect pests or weeds and their natural enemies.

A general comparison between North America (Nearctis) and Eurasia (Palearctis) reveals a rather close affinity between the vegetation of the two continents. Thus KUJALA (1945) estimates that about 600 species of plants are naturally common to the North American and European flora. These holarctic species belong, however, for the most part to primitive groups such as lichens, mosses and ferns, whilst among the arboreal plants, for instance, no species is native to both continents. This floristic affinity

between Nearctis and Palearctis is most pronounced in the northern areas, i.e. within the circumpolar tundra and the adjacent belt of northern coniferous forests (taiga). A similar view is expressed by LINDROTH (1957) for the non-marine animals, the number of species of which common to North America and Europe is thought to amount to some 5,000 or more.

This general floristic similarity is reduced if the vegetation of the deciduous forests and the more southern coniferous forests only is taken into account. Here the present European flora appears to be relatively poor when compared with that of North America. Thus 30 genera of plants are represented in the Nearctic zone of deciduous forests and that of eastern Asia, but not in that of Europe (GESSNER, 1942). According to a generally accepted theory (WALTER, 1954; ZIMMERMANN, 1942; KUJALA, 1945; LINDROTH, 1957; and others) this relative scarcity of the present European flora is caused mainly by the lack of convenient refuges for the more susceptible elements during the Pleistocene glaciations. This is well illustrated by the fact that many species and even genera of American distribution, nowadays totally absent from Europe, still existed there during the late Tertiary period (e.g. Tsuga canadensis, Thuya occidentalis, Pinus strobus (KUJALA, 1945)).

Intensive studies on North American forests within the distribution of Abies balsamea, i.e. on communities in which C. fumiferana may occur, have been carried out by KUJALA (1945) who, in comparing these forests of eastern Canada and the northeastern USA with those of Fennoskandia, draws the following conclusions:

(1) The North American vegetation of coniferous forests is different in the majority of species and is generally richer than that of Fennoskandia (especially in the arboreal plants, such as Tsuga, Thuya, etc.), but this difference at a specific level, and this richness of the North American forest vegetation, does not markedly affect the physiognomical and ecological similarity of the forests on both continents. (2) There is a true (phylogenetic) relationship between the forests of North America and those of Fennoskandia and this is not only reflected in the single components but also in the forests themselves, i.e. their structure and dynamics. (3) The present affinity is primarily the result of the persistence of the main elements originating from common ancestral forests, and not, or only secondarily, because of an exchange of species between North America and Fennoskandia. The North American forests west of the Continental Divide are rather different from those of eastern Canada (vicariant tree species !), but they do nevertheless also exhibit a close similarity to Palearctic forests.

The European beech-fir forests (Abieto-Fagetea) in which C. murinana is native do not belong to the zone of circumpolar coniferous forests which harbour the American C. fumiferana. These associations are restricted to the more temperate zone of deciduous forests where these are situated mainly on mountainous areas. The Atlanto-mediterranean silver fir, Abies alba, the host plant of the European fir budworm, is more similar in its ecological requirements to the Canadian Thuya occidentalis or even Tsuga canadensis than to A. balsamea. The European counterpart of A. balsamea, on the other

hand, may be seen in the boreal Picea abies, the main tree of the European and West Asiatic taiga (compare PSCHORN-WALCHER, 1956). A. alba itself is a rather ancient species*, fossils of which can be dated back to the Tertiary epoch (SAXER, 1955). In the early Pleistocene A. alba seems to have been present at least during one of the interglaciations in Middle Europe (fossils have been found near Luneburg, northern Germany (WALTER, 1954)), but it became totally extinct there during the glaciation periods. It survived in some still unknown refuges in southwestern or southeastern Europe and returned after the Pleistocene glaciations by two routes (passing west and east of the Alps) into Middle Europe. Its present occurrence there is consequently of very recent date. WALTER (1954) and SAXER (1955) estimate the age of Middle European fir forests as being about 8,000 to 9,000 years.

It is a well-known fact that migrations during the European glaciations brought about much contact between originally clearly separated vegetation zones. The special phenomenon of the contact and floristic exchange between the Atlanto-mediterranean fir forests and the boreal spruce forests, i.e. a part of the ancient circumpolar coniferous forest belt (taiga), has been studied by SAXER (1955).

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*Relict species of Abies found in the southern and southeastern parts parts of Europe, closely related to A. alba, indicate a wide distribution of an ancient Abies sp. in Europe, (SAXER, 1955). Similarly an ancient European distribution is assumed for the genus Cedrus, some relict species of which still occur in the Mediterranean area. C. atlantica in Morocco is one such remnant of a former European Cedrus sp. (WALTER, 1954). This is of interest in connection with the close relationship between the Middle European Apanteles murinanae (host plant: A. alba) and the North African A. dioryctriae (host plant: C. atlantica)(p. 84).

He indicates a very intimate connection between both these forest types in the mountainous regions of Middle Europe, where borec-alpine forests of Picea abies often occur directly above the Abies-Fagus zone. Obviously this contact between the two forest types must have facilitated exchanges of faunistic elements, especially those of the typical inhabitants of coniferous forests. For this reason the complexes of the European and American budworms may, in spite of their present occurrence in communities belonging to different life zones, be connected by earlier dislocations and movements of the European vegetation.

The generally accepted theory of a common origin of the majority of the Nearctic and Palearctic flora and fauna postulates an ancient connection between the present isolated continents. Geological and biogeographical data make it highly probable that one of these connections existed between Eastern Asia and North America (Bering land-bridge) during a period (or several periods) of glaciation (LINDROTH, 1957). The existence of one or several late (Pleistocene or Tertiary) transatlantic connections between North America and Eurasia either in the Wegnerian sense ("continental drift") or by assumption of one or several land-bridges ("bridge-theory") still seems to be open to discussion. It is accepted or taken into consideration by many zoologists and botanists (KUJALA, 1945; WALTER, 1954; JEANNEL, etc.) whilst others (REINSCH, 1942; GESSNER, 1942; LINDROTH, 1957) appear to be more inclined to explain the affinities between the Nearctic and Palearctic flora and fauna by the connection between Eastern Asia and America. LINDROTH (1957),

following extensive studies on the faunal connections between Europe and North America, denies "from a biogeographical point of view, the necessity for any kind of land connection in the past, directly joining the European with the American continent". The same opinion is expressed by DARLINGTON (1957). The biogeographical and geological evidence is apparently at present insufficient to provide a final solution to this problem. This, however, does not preclude the convincing hypothesis of a common origin for the main elements of the North American and Eurasian coniferous forests.

The budworm parasites dealt with in this study are a part of the European and North American coniferous forest communities whose relationships have been outlined above. For a biogeographical evaluation of these parasite complexes it becomes necessary to summarize their systematic affinities. A total of 35 genera of parasites is given in Table 8. Two of these include a species, which probably occurs both in North America and in Europe (the Tachinids Nemorilla maculosa and Winthemia amoena, the latter being only a parasite of Choristoneura in North America*. Thirty-two parasite genera are represented in both Europe and North America. (The closely related Tranosema arenicola and Horogenes cacoeciae are here considered as cogeneric species (p. 81)). Two European Ichnuemonid genera, members of which parasitize the fir budworm, have not as yet

*Another holarctic species is probably the Ichneumonid Theronia atalantae (Poda), which is occasionally recorded from the spruce budworm (MUESEBECK et al., 1951). To date it has not been bred from the fir budworm, but it is well known as a parasite of other European forest Lepidoptera.

been recorded from North America. These are the monotypic genus Cephaloglypta which may, however, be considered as being only a specialized descendant of the holarctic genus Glypta, and the genus Blaptocampus, which is not listed in MUESEBECK et al. (1951, 1958). It cannot be decided at present whether this absence of Blaptocampus from the American list is due to different taxonomic conceptions—as is the case with the closely related Agrypon (MUESEBECK et al., 1958)—or if the genus concerned is really absent from North America. In any case, however, a holarctic distribution is found in closely related genera such as Anomalon Panzer, etc. According to MESNIL (personal communication) the Tachinid "Erynnia" tortricis is a member of a new genus not represented in Europe but closely related to the widespread holarctic genus Nemorilla. Thus, nearly all of the genera of the European budworm parasites are represented in North America, and nearly all of the genera of the American spruce budworm parasites complex occur in Europe.

Twelve genera of hymenopterous parasites, including almost all the important species, are found both in the European and American budworm complexes, whilst members of the remaining eight hymenopterous genera which have been bred exclusively from one of the two hosts are generally of minor importance. Moreover, many of them have been reared from host species inhabiting the same communities as C. murinana (e.g. Trichogramma spp., Dicladocerus sp., Elachertus sp., Tetrastichus spp. and Exochus sp. have been observed attacking European Microlepidoptera in coniferous forests). Many of the cogeneric hymenopterous parasites of the European and American

budworms are closely related (p.101) and some among them, like Phaeogenes maculicornis and Ph. hariolus or Apechthis resinator and A. ontario could perhaps even be considered as being of only subspecific rank. Host ranges, ecological preferences, bionomics and other biological features parallel the close morphological relationships of the hymenopterous parasites associated with C. murinana and C. fumiferana.

A somewhat different situation is encountered in the dipterous parasites: here only members of four genera attack both hosts, the majority of them being of negligible importance whilst species belonging to eight genera, including very important parasites, have been bred from only one of the two host species, i.e. almost exclusively from the American C. fumiferana. But here, too, nearly all the genera are of European-North American distribution*.

If these relationships between the European and North American budworm parasites, especially the Hymenoptera, are compared with the general floristic and faunistic affinities of the corresponding

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*The peculiar difference between the complex of Tachinids and that of the Hymenoptera has already been mentioned (p. 91). An explanation of this is not possible in the framework of the present study. According to MESNIL (personal communication) solution to this problem could perhaps be found in the fact that the Tachinids as a whole have their centres of origin in more southerly areas and that, very probably, part of the present European and North American Tachinid fauna immigrated there from subtropical or tropical regions. The centre of origin of many of the hymenopterous genera concerned may, on the other hand, be situated in temperate or even boreal zones of the northern hemisphere. Thus the hymenopterous genera concerned would be more closely connected geographically than the dipterous parasites and this could explain the higher degree of ecological and biological similarity.

regions, the following conclusions may be drawn:

(1) It is a general rule that in most cases speciation of the European and North American forms with common Tertiary ancestors did not split the ancient genera existing before the topographical separation. This becomes quite obvious if corresponding lists of the boreal and temperate zones of Europe and North America are compared (KUJALA (1945): higher plants; MUESEBECK et al. (1951): Hymenoptera; LINDROTH (1957) and other authors: mammals, birds, insect orders such as beetles, butterflies, etc.).

The same is true for almost all of the 35 genera of the Ichneumonids, Braconids, Chalcids and Tachinids involved in the two Choristoneura complexes.

Many of the European and American elements have, during their separate evolution, not even varied beyond the specific level; they have only given rise to new subspecies. As examples the carnivorous mammals Alopex lagopus (L.), Canis lupus L., Felix lynx L., Gulo gulo (L.), Mustela erminea L., Mustela nivalis L., Ursus arctos L., Vulpes vulpes (L.) may be mentioned.

Similar cases occur in the budworm complexes, some parasite species being apparently native to both Europe and North America, whilst others are so close to each other that the differences between them appear no larger than acknowledged variations occurring over their European distribution (e.g. the Ichneumonids Itoplectis alternans (Grav.) and I. alternans var. kolthoffi (Auriv.)).

Thus the systematic relationships between corresponding European and North American budworm parasites are of about the

same degree as that in the majority of analyzed groups of plants or animals in the two areas. Speciation of the topographically separated forms generally did not exceed the generic level, and several of the present palearctic and nearctic species still clearly reveal their common origin.

(2) American elements without European counterparts, such as the tree genera Thuya, Tsuga, Pseudotsuga, etc., and the bird families Parulidae (warblers) and Vireonidae (vireos) which play some part in reducing C. fumiferana populations (FRANZ, 1957), must either be considered as remnants which have become extinct in Europe or as immigrants which invaded the coniferous forest belt from more southern parts of America (REMSCH, 1942). It is perhaps noteworthy that no such element occurs among the insect parasites of C. murinana and C. fumiferana. Practically no relict or new form without a congeneric relative in the European coniferous forests has been found within the parasite complex of American spruce budworm.

This might be principally due to the close affinity between the host species*. However, in the author's opinion this also indicates a certain continuity and uniformity of the ecological conditions within the coniferous forest communities concerned, and a rather marked persistence and conservatism of the insect parasite groups

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*The importance of the systematic relationship of the hosts is indicated by the fact that North American phytophagous insect genera without European counterpart (e.g. Leptinotarsa (Col.), Hyphantria (Lep.)) are to a certain extent associated with entomophagous parasite genera which are absent from Europe (e.g. the Tachinids Dorychorophaga sp., parasitizing L. decemlineata Say, or Lespesia sp., Zenillomyia sp. and Eusisyropa sp. parasitizing H. cunea Dru.)(MESNIL, personal communication).

adapted to these communities.

(3) This latter view is supported by the fact that the close affinity of the European and North American budworm complexes is accompanied by a close similarity of the parasites of the north-eastern and northwestern American spruce budworm populations, which are not only topographically separated but also occur on other host plant species (Abies balsamea and accompanying coniferous trees in eastern Canada, Maine and New York (JAYNES & DROOZ, 1953) as compared with Pseudotsuga taxifolia in western Canada (WILKES, 1946)). Although three parasite species are only recorded from the western C. fumiferana populations (WILKES, (1946): Phytodietus fumiferanae, Ceromasia auricaudata and Clemelis incrassata) the general correspondence between the eastern and western parasite complexes is obvious (compare WILKES et al. (1948) with DOWDEN et al.(1950), etc.), especially if the distances separating them and the phytogeographical differences are taken into account.

Another demonstration of the relative conservatism of the insect parasites concerned is the striking similarity between the spruce budworm complex and that of the Jack-pine budworm, C. pinus (p. 75). C. fumiferana and C. pinus are two closely related, sympatric species in which, according to SMITH (1953), in addition to normal absence of cross-mating the females differ in their host tree preferences for oviposition (Abies spp., Picea spp., Pseudotsuga sp., etc., versus Pinus banksiana and P. resinosa) and to a certain extent in their phenology. These "isolation factors"—ecological, temporal and sexual—prevent introgressive hybridisation in nature and operate,

therefore, as evolutionary factors. Specialized budworm parasites (Apanteles, Glypta) and species with a restricted host-range, such as Phaeogenes hariolus, which all occur both on C. fumiferana and C. pinus must be subject to the same ecological and phenological isolation as their hosts, yet no splitting up of these parasites has so far been observed.

(E) Predisposition and specialization

It has already been stated that a specific phylogenetic parallelism does not exist among the European and American budworm parasites and that, consequently, the specialization in budworm parasites such as Apanteles, Glypta and Phytodietus is probably of relatively recent origin (p. 109). There is, on the other hand, a striking ecological parallelism between individual parasite species such as Phaeogenes maculicornis and Ph. hariolus, Apechthis resinator and A. ontario, etc. These pairs are not only morphologically very similar, but also show corresponding ecological restrictions to hosts in forests or on coniferous trees (pp. 93, 97). Here it seems highly probable that their common ancestors were already specialized as "woodland forms" associated with hosts in coniferous forests, and this is further supported by the Tertiary history of palearctic forests (KUJALA, 1945; RENSCH, 1949). If all the relationships between the European and North American budworm parasites are taken into account (p. 100), the conclusion seems to be justified that the ecological restrictions of the parasites concerned, i.e. their association with hosts in coniferous forests,

is of a more ancient date than their biological specialization on Choristoneura spp.

The single parasite species occupy different ecological niches in the communities they inhabit. This is well demonstrated by the three Phaeogenes spp. (maculicornis, invisor, nanus) in the observation area in the Vosges. These three parasites are restricted to microlepidopterous pupae on fir, oak and in the litter of the soil, respectively. Again Apanteles murinanae is restricted to microlepidopterous larvae feeding on or in the needles and buds of fir. These different ecological ranges and host-ranges of the parasite species within a given community form in toto a complicated network closely correlated with the single ecological niches of the biocoenosis. This statement must be qualified since several niches seem to be only incompletely occupied (e.g. lack of egg parasites in C. murinana) and since, obviously, a certain plasticity in the psychic pattern of ovipositing parasite females may sometimes lead to unexpected distribution of insect parasites among their hosts (ZWOLFER & KRAUS, 1957). On the whole, however, it appears reasonable to consider the insect parasite fauna of communities such as the North American balsam fir forests or the European fir-beech forests as physiologically and ecologically segregated systems of species which are more or less adapted to the single host species and stages within the various niches.

This predisposition of entomophagous parasites to host species belonging to certain systematic groups and occupying certain habitats becomes particularly evident when some introduced insect pests are

considered. For example, the omnivorous leaf-tier Cnephasia longana (Haw.) may be mentioned. This European Tortricid has been accidentally introduced into North America where it has become a pest of strawberries and other crops. EDWARDS & MOTE (1936) mention the following American parasites from C. longana in Oregon: Phytodietus burgessi (Cress.), Glypta sp., Horogenes eureka (Ashm.), Microbracon hyslopi (Vier.) and M. gelechiae Ashm., the last being the most important species. Our own rearings of several Cnephasia spp. from Middle Europe (C. virgaureana Tr., Chrysantheana sensu Obr., Cnephasiella incertana (Tr.)), which are biologically closely related to C. longana and which, to a certain extent, attack the same host-plants (strawberry), produced a number of corresponding species: Phytodietus ? polyzonias, Horogenes sp. and other closely related Campoplegini, and Microbracon stabilis Wesm., the last being the most important parasite. A Glypta sp. (G. ceratites) was not reared from Cnephasia itself but from Olethreutes lacunana larvae in leaf-rolls of strawberry, i.e. in the same ecological niche as Cnephasia spp. In North America the parasitism of the introduced C. longana by a series of native species which correspond to European parasites of Cnephasia spp. is certainly not a matter of chance, but a consequence of a similar physiological and ecological predisposition of related European and North American insect parasites.

From the evidence given in Section VI it may be assumed that the similarities between the complexes of the fir and spruce budworm are for the most part caused by such a parallel physiological and ecological preadaptation of European and North American parasites.

It has been stated that this general biological predisposition occurs to a certain extent in several taxonomically unrelated members of the same genus or tribe, for instance in Cephaloglypta sp., Glypta fumiferanae and G. cicatricosa. In this way specializing on budworms as hosts systematically distinct species may occupy corresponding niches (convergent adaptation in the Glyptini spp. and in Apanteles spp.). In a third parasitic genus, Phytodietus, this predisposition is again indicated by parasitism of both Choristoneura spp. by European and American species, but here only an American member (Ph. fumiferanae) succeeded in becoming specialized and even this specialization took place only in the western parts of North America.

The process of specialization itself may be divided into two components; restriction of the host-range and of the ecological range on the one hand, and increasing adaptations to a given host in host-searching behaviour, oviposition, and in the life-cycle on the other hand.

Single steps of this process are to be observed in many of the fir and spruce budworm parasites. A parallel increase in the ecological restriction and restriction of the host-range is, for instance, shown in the following series of European and American budworm parasites: Pimpla turionellae - Itoplectis maculator - Ephialtes inquisitor - Apechthis rufata - A. resinator - Phaeogenes maculicornis (parasites of the fir budworm) and I. conquisitor - Scambus (Ephialtes) hispae - A. ontario - Ph. hariolus (parasites of the spruce budworm). Adaptations in searching behaviour seem to occur in I. maculator (p. 51) and probably in other budworm

parasites.

These single steps of ecological restriction and adaptation have resulted in the relatively great regularity with which many of the non-specialized European and American budworm parasites are associated with the Choristoneura spp., but only in the members of three genera or tribes, respectively, has this trend led to a true specialization.

It is obvious that species of the Glyptini, Phytodietus and Apanteles offered especially favourable opportunities for becoming specialized on the Choristoneura spp. Glypta spp. are mainly parasites of Tortricids, and are frequently highly specialized in their mode of oviposition which enables them to attack very young host larvae in protected sites. Furthermore, they are associated with the host attacked for a long period during the season and thus they avoid the necessity for host alternation (compare CAMERON, 1938). Similar features to those shown by Glypta exist in the Apanteles spp., many of which also show a highly developed host-searching ability, parasitism of young host larvae, and a univoltine cycle. In contrast to the endoparasitic Glypta and Apanteles spp. the ectoparasitic Phytodietus spp. only feed on their hosts for a relatively short period, but here too a specialized mode of oviposition (which prolongs the time of direct connection with the host) (BALTENSWEILER & MOREAU, 1957; SIMMONDS, 1947) and the possibility of hibernating within a rather strong cocoon facilitates the synchronization between parasite and host. These biological characteristics do not explain why only the species mentioned have

become specialized on the European and American budworms, but they demonstrate the greater biological preadaptation to specialization in Glypta, Apanteles and Phytodietus when compared with other budworm parasites (Pimplini, etc.) with their less restricted oviposition habits, their relatively short period of connection with the host, and their less well-marked synchronization.

As a consequence of the constant association with the host and the prolongation of the larval periods, the specialized parasites become themselves subject to considerable secondary parasitism, either by typical hyperparasites of the community (which mainly attack Apanteles spp.) or by interaction with less specialized primary parasites of the budworms (which affect the Glyptini, and to a certain extent also Phytodietus fumiferanae (COPPEL, 1951)). The secondary nature of these interactions becomes apparent from a consideration of the parasitism of the specialized Cephaloglypta murinanae by the much less specialized Itoplectis maculator. The latter species is primarily attracted to the fir budworm. There it meets with Cephaloglypta which secondarily becomes preferred to the primary host, whilst other Glypta spp. of the community are relatively neglected by the I. maculator population (p. 51).

An attempt has been made to summarize the hypothetical evolutionary trends of the fir and spruce budworms and their parasites in Table 9.

Based on the results of a single study only the conclusions outlined above cannot pretend to cover all the problems of the evolution of insect parasite complexes, but it is hoped that some general principles—especially the importance of ecological and

physiological predisposition—involved in the formation of parasite complexes have been indicated. It would be a very worthwhile study to undertake similar work on entomophagous insects associated with other host groups and to intensify this method of comparative study.

VIII. Summary

The more important elements of the parasite complexes of the European fir budworm, Choristoneura murinana, and the North American spruce budworm, C. fumiferana are relatively very constant both in space and time over the entire distribution ranges of the hosts. This and the obvious similarity of the lists of parasites of the two budworm species prompted this study which is an attempt to gain some insight into the general structure and evolution of the host-parasite associations among insects by a comparative evaluation of available data in these two complexes.

The first part of this paper deals with the composition, biology and ecology of the parasite complex of C. murinana, and compares each parasite species of this host with the corresponding one of C. fumiferana. The results of this comparison from parasitological, biogeographical and phylogenetical view-points are then discussed.

The primary parasites of the fir budworm have been arranged into three groups according to their constancy and relative abundance in the complex:

I. Dominant species, very constant and often abundant

(Cephaloglypta murinanae, Apanteles murinanae, Phaeogenes maculicornis, Itoplectis maculator).

II. Common species of minor importance (Pimpla turionellae, Apechthis resinator, A. rufata, Ephialtes inquisitor, Monodontomerus aereus, Blondelia nigripes).

III. Occasional parasites (21 recently observed species, many others mentioned in former literature).

Notes on the biology, hyperparasitism, constancy, abundance, host-preference and ecological range of the dominant and common parasite species of C. murinana are given. A list of 14 hyperparasites is included.

The relative uniformity with regard to parasites in all the European fir budworm infestations investigated to date corresponds to that of the North American spruce budworm complexes (McGUGAN & BLAIS, 1959), and also to the regularity in this regard of some other intensively studied host-parasite or host-predator associations (European parasite complex of Operophtera brumata, European predator complex of Dreyfusia piceae, etc.). The constancy of the fir budworm parasite complex calls attention to the ecological and biological ranges of the individual species, and this is discussed in Section IV (B).

If the various host-ranges of C. murinana parasites are considered together with their host preferences and their position in the complex, five types of combinations occur (Fig. 3): (1) Species with a restricted host-range which, at least during mass outbreaks, concentrate on C. murinana (the univoltine Apanteles murinanae,

Cephaloglypta murinanae, Phaeogenes maculicornis). (2) Species with a wide host-range (polyvalent species) concentrating on C. murinana during mass outbreaks (the multivoltine Itoplectis maculator). (3) Species with a wide host-range attacking C. murinana regularly but without particular preference for this host species (Pimpla turionellae, Apechthis resinator, E. inquisitor, etc.). (4) Ecologically restricted species with a preference for other hosts in other niches of the community from which they occasionally pass to C. murinana (Tranosema arenicola, Phytodietus polyzonias, etc.). (5) Species with a wide host-range attacking C. murinana only exceptionally (Pimpla instigator, Itoplectis alternans, etc.).

Ecological (strictly speaking ethological) limitations of the potential host-range totally or partly exclude a number of polyvalent species which are physiologically quite suitable as parasites of C. murinana. The same factors, however, favour another group of polyphagous species which occur in the same ecological niche as this host. By comparing different parasite rearings and the results of transfer experiments, two types of ecological restrictions have been found in the complex of C. murinana: (1) Restrictions of the potential host-range by preference exerted by the parasite for certain host plants or groups of host plants, e.g. Apanteles murinanae, Cephaloglypta murinanae and Phaeogenes maculicornis, occurred in the observation areas only on hosts on Abies, and Itoplectis maculator distinctly preferred such hosts. In the Vosges area Apechthis rufata attacked fir budworm pupae only when artificially transferred to oak leaves. Tranosema arenicola and

Phytodietus polyzonias parasitized various Tortricid larvae living on Quercus and other deciduous trees but were found only in exceptional cases in C. murinana on fir. Corresponding observations have been made for Ephialtes calobata and Actia maksymovi. (2) Restrictions of the potential host-range by a preference by the parasite for certain strata of the community: the dominant parasites of Cephalcglypta murinanae and Phaeogenes maculicornis seem to prefer fir budworm larvae in the regions of the crowns of the trees. Several other species (Triclistus globulipes, Blaptocampus nigricornis, Agrypon variitarsum, Chorinaeus longicornis) have been reared exclusively from material from young firs and fir thickets.

Some inter-relationships between the complex of C. murinana and other hosts of the community are discussed and lists are given of other Tortricids and species belonging to related groups found together with C. murinana.

The sex-ratio of several of the parasites reared from C. murinana is related to their host preference. It varies greatly in Itoplectis maculator, reared from different host species, the proportion of female offspring being highest when the most preferred host, Cephalcglypta murinanae, is parasitized. The sex-ratios found in Apechthis rufata indicate an influence of the preferred oviposition site. From C. murinana on fir either no (Vosges area) or comparatively few A. rufata have been reared, males always being much more frequent than females. From C. murinana transferred to oak, the preferred oviposition site in the Vosges area, only females emerged.

For the purpose of comparing the parasite complexes of C. murinana and C. fumiferana a survey of the parasites of the latter species and of the Jack-pine budworm, C. pinus, has been compiled from the recent literature (Section V.).

When the average degree of parasitism of corresponding groups of fir and spruce budworm parasites is compared (Table 7) mortality caused by Apanteles, the Glyptini and pupal parasites (Ichneumonids) is seen to vary similarly within corresponding ranges in both Europe and North America. Egg parasitism has so far been observed only in North America. Mortality of mature larvae caused by Tachinids and Meteorus spp. is negligible in Europe, but often becomes important in North America.

The majority of the fir and spruce budworm parasite species belong to the same genera or tribes (Table 8). The corresponding European and American species are compared here with regard to their systematic relationship, abundance, host-range, and ecological preference. The results of this comparison are summarized on p. 100. The highly specialized and biologically closely corresponding parasites Apanteles murinanae and A. fumiferanae and Cephaloglypta murinanae and Glypta fumiferanae show no direct phylogenetic relationship; the similarity of their biologies is a result of adaptive convergence from systematically separated ancestors. About 20 corresponding European and North American parasite species are morphologically and biologically rather similar with a normal cogeneric relationship. Only few of these related species hold an equivalent position in the two budworm complexes, the majority

having only a superficial correspondence which is not reflected in their abundance, constancy or importance. Seven Choristoneura parasites occur on the two continents and are either identical (Nemorilla maculosa) or are systematically very closely related (i.e. more similar to each other than to other members of the genus). These sibling species are Phaeogenes maculicornis - Ph. hariolus, Amblymerus subfumatus - A. verditer (both pairs of species with a similar position in the Choristoneura complexes) and Apechthis resinator - A. ontario (dissimilar position).

Since insect parasites (= parasitoids) are somewhat different from the majority of other animal parasites ("true parasites"), the evaluation of the data presented in the previous sections was prefaced with a short discussion of some of the differences between parasitoids and "true parasites". In parasitoids the parasitic period on the host and the free-living period in the community may, generally speaking, be considered as of about equal biological rank. The effect of the environment on the evolution of parasitoids is obviously greater than in the case of true parasites. The distribution of the progeny is often at random with true parasites whilst with parasitoids the psychic pattern of the adult female generally plays a primary role (BAER, 1952). Small changes in the psychic mechanism of the mature female may consequently have a considerable influence on the host range and other aspects of the evolution of parasitoids. The food supply for the parasitic stages is generally much less with parasitoids than with true parasites and this indicates a greater role played by competition in the former

group (BAER, 1952).

With the Choristoneura complexes phylogenetic parallelism in the evolution of parasites and hosts can be seen only in the correlation of higher categories but not at specific level. An explanation for this lack of specific phylogenetic parallelism may possibly be found in the probable relatively recent origin of biological specialization in the Choristoneura parasites concerned (Apanteles, Glyptini, Phytodietus).

The general biogeographical relationships of the communities inhabited by C. murinana and C. fumiferana are outlined in Section VII (D). The European beech-fir forests (habitat of C. murinana) do not belong to the same vegetation zone as the North American coniferous forest belt (habitat of C. fumiferana) and the present biocoenoses harbouring C. murinana north of the Alps are of very recent origin, their elements having suffered much disturbance during the Pleistocene glaciations. Nevertheless, a high correlation occurs in the composition of the European and North American Choristoneura complexes. In contrast to several remnant or newly immigrated North American plant genera or families of birds, etc., which do not now possess any representative members in Europe, almost all of the 35 genera of insect parasites of the fir and spruce budworms are at present represented in both continents. Within the North American continent the topographically separated eastern and western spruce budworm populations (living on different host tree species) are widely attacked by identical parasite species, and the same is true for the related Jack-pine budworm. This indicates not only a certain

ecological uniformity and continuity of the coniferous forest communities concerned but also a rather high degree of persistance and conservatism of the insect parasite groups adapted to these communities.

The lack of specific phylogenetic parallelism in the Choristoneura parasites, and the often striking ecological parallelism (found for example in Phaeogenes spp., Apechthis spp., etc.), lead to the conclusion that the ecological preference (association with hosts on coniferous trees) of the parasites concerned has in general antedated their biological specialization on the two host species. Among a limited number of European and North American parasite species ecological preferences and physiological adaptations combine to form a certain predisposition to attack Choristoneura spp. The occurrence of such a predisposition is discussed in connection with some observations on the European and North American parasites of Cnephasia spp. The conclusion is drawn that a parallel predisposition of certain parasite species on both continents, and an equivalence of the "parasitological niches" offered by the fir and spruce budworms is the main or only reason for the great similarity between the hymenopterous parasites of the two Choristoneura spp.

Several of these ecologically and physiologically predisposed parasite species show a tendency to become biologically specialized. The process of this specialization includes two components: restriction of the ecological range and the host-range on one hand, and increasing behaviouristic and biological adaptations on the other. Single steps of this process may be seen in many species.

Thus a parallel increase of ecological restriction is shown by the following series of European and North American budworm parasites: Pimpla turionellae - Itoplectis maculator - Ephialtes inquisitor - Apechthis rufata - A. resinator - Phaeogenes maculicornis (parasites of the fir budworm) and I. conquisitor - E. hispae - A. ontario - Ph. hariolus (parasites of the spruce budworm). True specialization, however, has only been reached by members of the genera Apanteles, Phytodietus and Glypta (sensu lato), whose special preadaptation to this process is shortly discussed.

Finally, specialization is followed by secondary interactions between less specialized and highly specialized budworm parasites, or between the latter and hyperparasites of the community. These interactions occur in the complex of the fir budworm as well as in that of the spruce budworm; in the former, however, it would seem that they exert a more adverse effect on the specialized forms.

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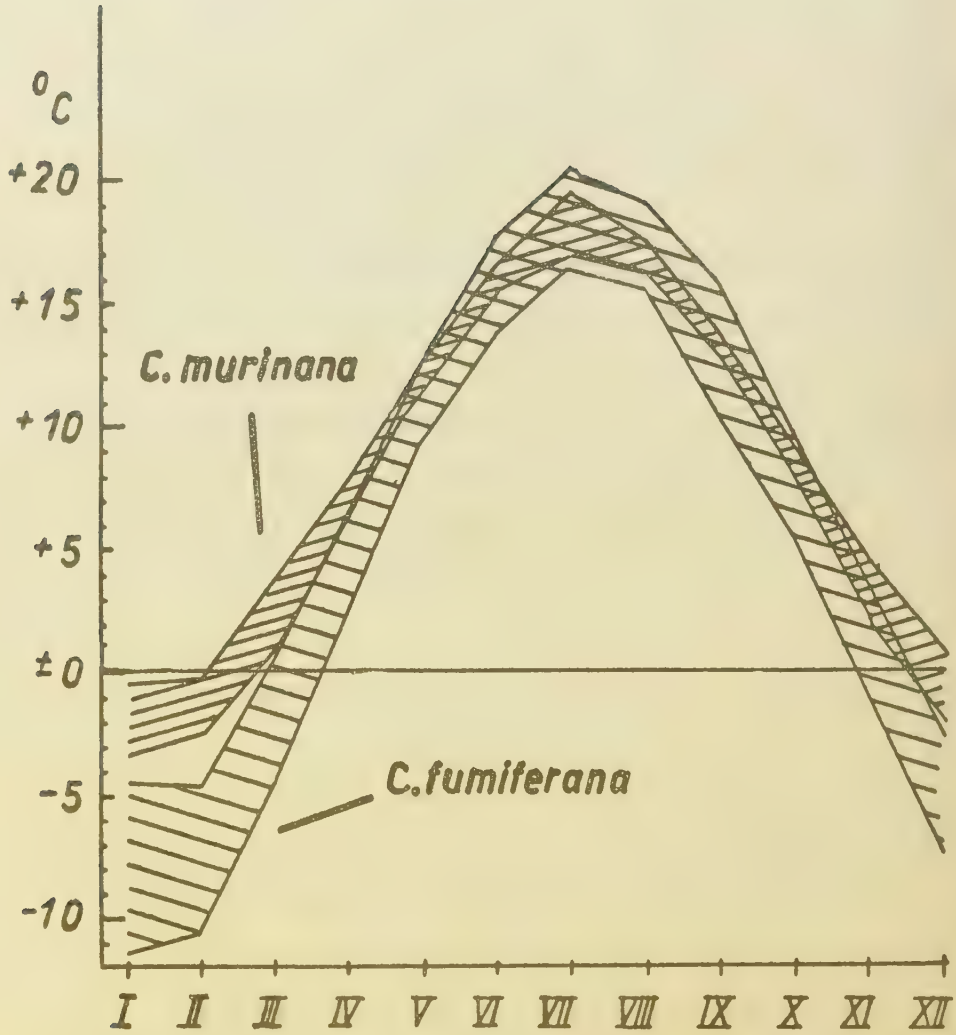

Fig. 1 Ranges of monthly average temperatures in areas inhabited by C. murinana (eastern France, western Germany, eastern Austria, CSR, Poland) and C. fumiferana (Quebec, Ontario, New Brunswick, Maine, New York, British Columbia)(MORGENTHALER, 1952)

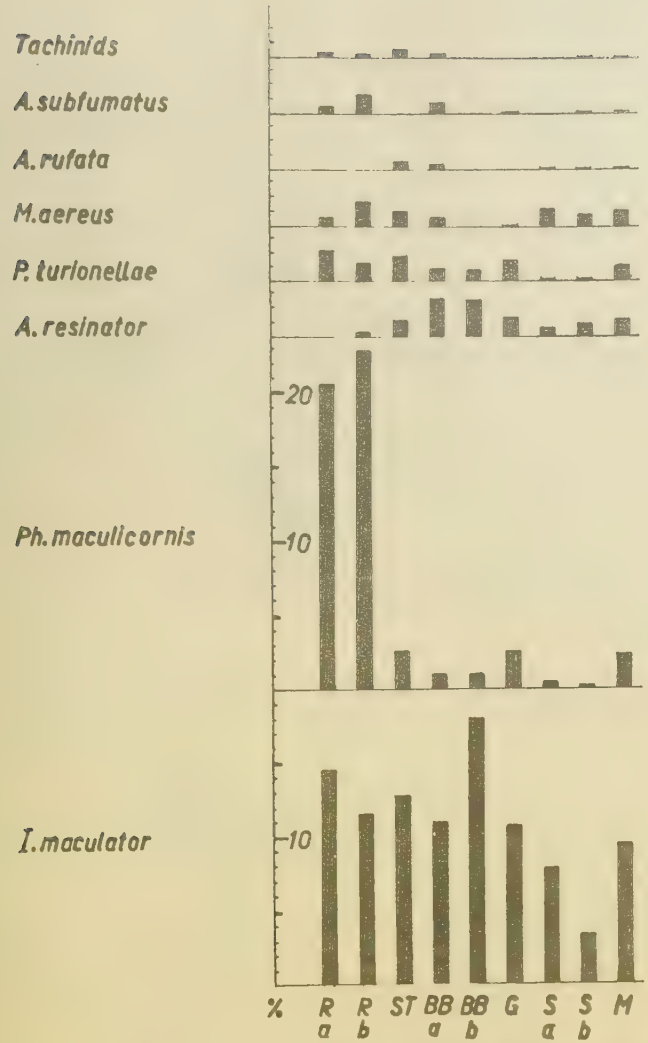

Fig. 2 Relative abundance of pupal parasites of C. murinana (percentage of parasitism based on the pupal population of C. murinana). Localities: Ra = Ribeauville (Vosges) (1955); Rb = Ribeauville (Vosges)(1956); ST = Staufen (southern Black Forest)(1956); BBa = Baden-Baden (northern Black Forest)(1956); BBb = Baden-Baden (northern Black Forest), FRANZ et al. (1958); G = Gernsbach (northern Black Forest), FRANZ et al.(1958); Sa = B. Stiavnica (Slovakia)(1956); Sb = B. Stiavnica (Slovakia), CAPEK et al. (1958); M = mean value

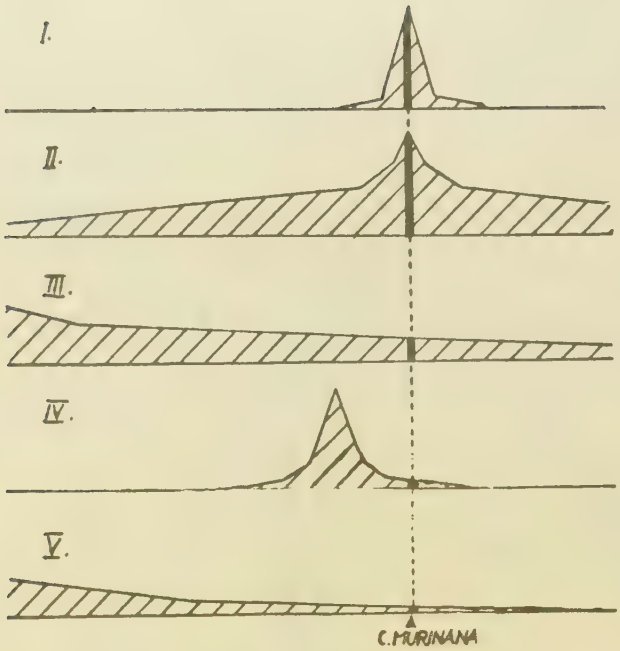

Fig. 3 Types of combinations between host-range and host-preference among parasites of C. murinana. (Explanation pp. 49-53

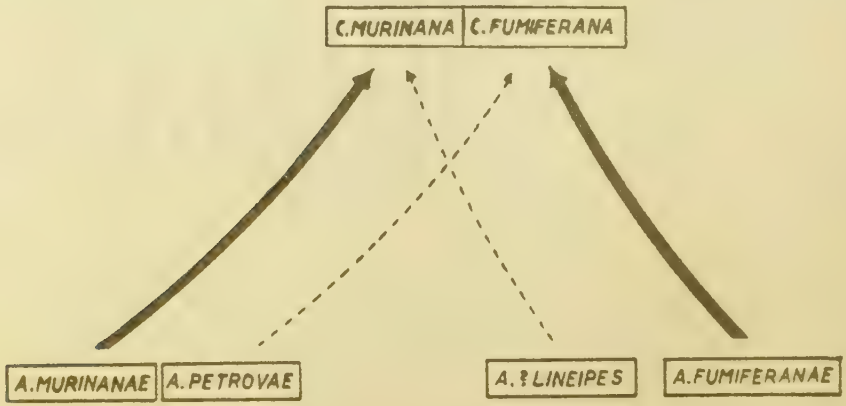

Fig. 7 Scheme of the hypothetical evolutionary trends of the Apanteles spp. parasitic on the two Choristoneura spp. (pp. 81-83)

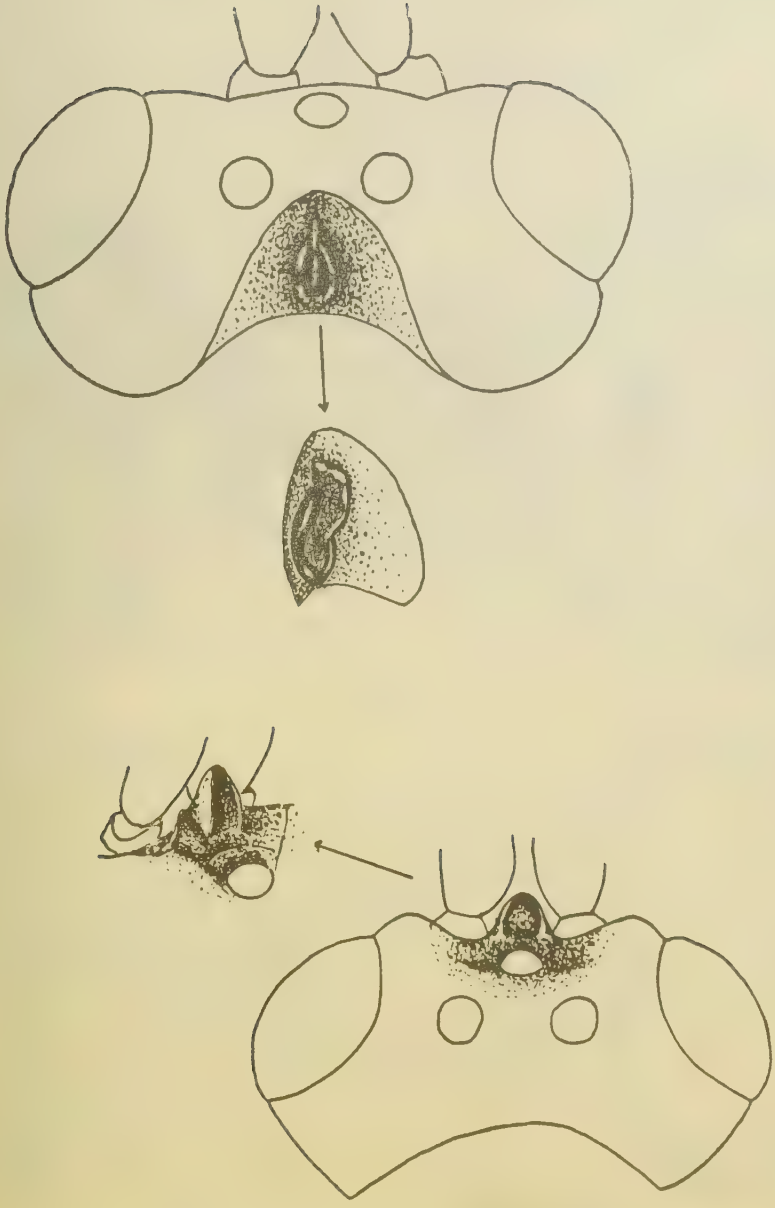

Fig. 4 Structures on the head of Cephaloglypta murinanae (above) and Glypta fumiferanae (below)(p. 78)(♀♀)

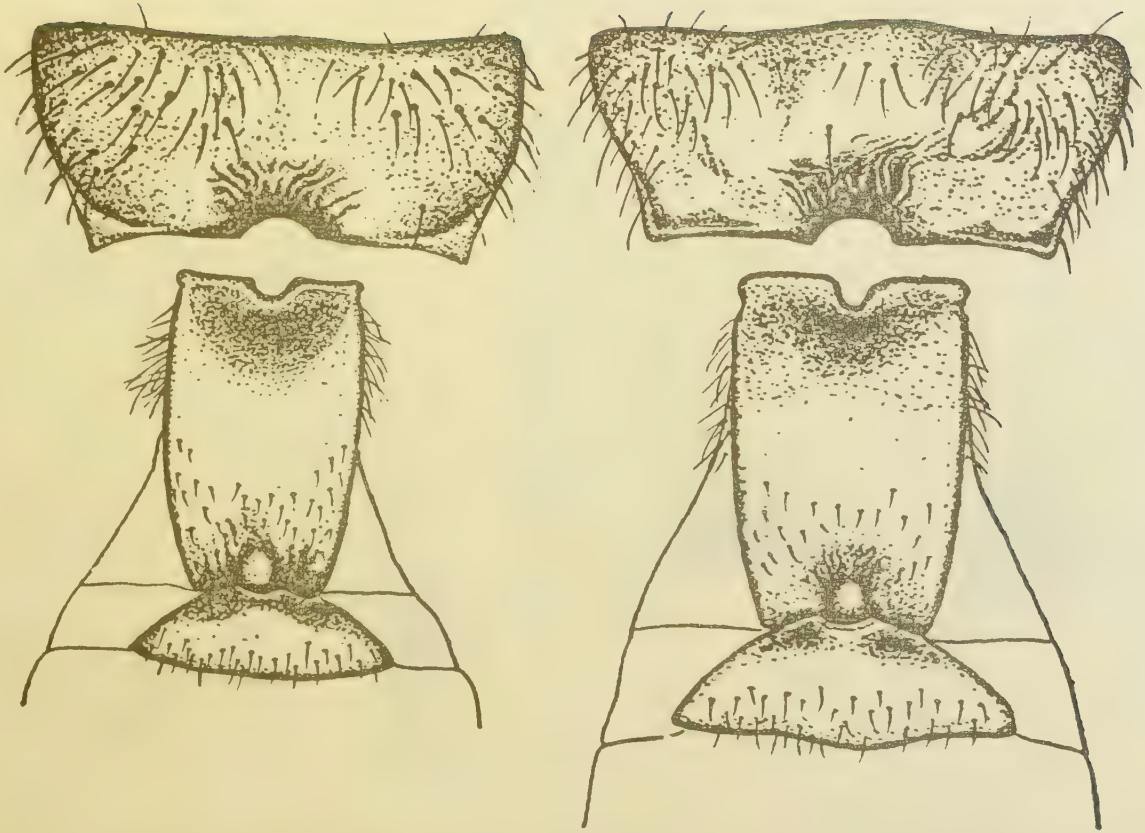

Fig. 5 Propodeum and first two abdominal segments of Apanteles petrovae and A. murinanae (♀♀)(p. 82) Left: A. petrovae; right: A. murinanae

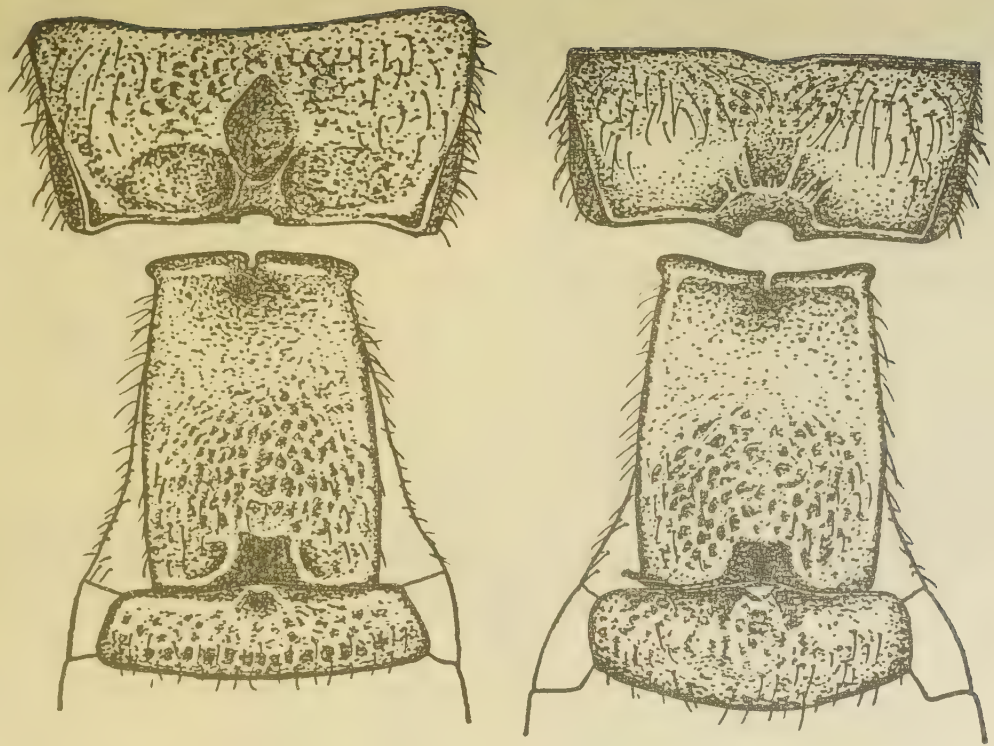

Fig. 6 Propodeum and first two abdominal segments of Apanteles fumiferanae and A. ? lineipes (♀♀)(p. 82) Left: A. fumiferanae; right: A. ? lineipes

TABLE 1: List of parasites species with three or more records from C. murinana. xxx = first in importance. xx = second in importance * emerging from host pupae ** emerging from host larvae

Pupal parasites*		KOLUBAJIV (1934) Moravia	SCHIMITSCHECK (1936) Vienna Forest	FRANZ (1940) Southern Black Forest	SCHIMITSCHECK (1943) Moravia	BUCHER (1953) Northern Black Forest	BUCHER (1953) Vosges	ZWOLFER (1956) Vosges	ZWOLFER & KRAUS (1957) Vosges	Present Investigations Southern Black Forest (1956)	Present Investigations Southern Black Forest (1957/58)	Present Investigations Northern Black Forest (1956)	FRANZ et al. (1958) Northern Black Forest (Baden-Baden)	Northern Black Forest (Germsbach)	CAPEK et al. (1958) Slovakia	CIBC Material Slovakia (1956)	WIACKOWSKI (1957) Poland
Itoplectis maculator	Ichn.	xxx	xxx	xxx	xx	xxx	xxx	xx	xx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xx
Pharongenes maculicornis	"	xx			xxx	xx		xxx	xxx	x	x	x	xx		x		xxx
Apechthis resinator	"	x					xx		x	xx	xx	xx		x	xx	x	x
Pimpla turionellae	"	x	x		x	x		x	x	xx		x		x	x	x	
Apechthis rufata	"	x	x	xx	x		x			x	x	x					x
Tricistus globulipes	"						x	x				x					
Acrypon varitarsum	"						x	x	x	x	x	x		x	x	x	
Mongolontomerus aereus	Chal.			x	x		x	x	x	x	x				x	x	x
Amblymerus subfumatus	"							x	x			x			x		
Blondelia nigripes	Tach.	x	?	?	x		?	x		x	x	x			x	x	?
Bessa funax	"								x								
Nemorilla maculosa	"	x					x	x		x	x				x	x	
Larval parasites**																	
Cephaloglypta murinanae	Ichn.	?	?	xxx	xxx	xxx	xxx	xxx	xxx	xx	xx	xxx	xxx?		xx	xx	?
Ephialtes inquisitor	"			x	x			x	x	x		x				x	
Ctenodictus polyzonias	"	x				x	x	x	x							x	
Apanteles murinanae	Brac.	x	?	?	?	?	?	xx	xx	xxx	xxx	xx	xx?		xxx	xxx	?
Meteorus ruficeps	"					x	x								x		

TABLE 2: Parasites bred from C. murinana in 1955 and 1956 (Vosges, southern and northern Black Forest & Slovakia)

* i.e. parasites killing the pupal stage of the host
** gregarious parasites, only the number of hosts killed is given

Groups	Larval Parasites	n	%	Pupal Parasites*	n	%
Dominant species	Cephalogłypta murinanae Apanteles murinanae	947 314		Itoplectis maculator Phaeogenes maculicornis	2466 606	
% of total parasitism			95.4			77.4
Species of minor importance but occurring regularly	Ephialtes inquisitor	30		Apechthis resinator Pimpla turionellae Monodontomerus aereus Blondelia nigripes Apechtis rufata	287 240 240** 18 30	
% of total parasitism			2.3			20.6
Irregular and occasional species	Ephialtes palpata Tranosema arenicola Phytodietus polyzonias Glypta cicatricosa Bessa fugax Meteorus sp. Nemorilla maculosa Actia maksymovi Glypta spp.	4 3 3 2 2 1 2 1 12		Amblymerus subfumatus Blaptocampus nigricornis Triclistus globulipes Agrynon variitarsum Chorinaeus longicornis Ichneumonid sp.	36** 12 7 6 6 3	
% of total parasitism			2.3			1.9

TABLE 3: Parasitism by I. maculator on host species on fir and oak (Vosges - June 20-30, 1956) in the same locality

Hosts	Host plant: fir	Host plant: oak
Tortricids	(C. murinana) 11.5% parasitized	(A. xylosteana, crataegana) (T. viridana, P. ribeana) 1% parasitized
Cocoons of Glypta spp.	28% parasitized	No parasitism
Cocoons of Tachinids	Some parasitized	No parasitism
Cocoons of Tranosema arenicola	All 3 parasitized	No parasitism
Cocoons of Meteorus sp.	Some parasitized	No parasitism

TABLE 4: Parasitism of hosts on fir and oak by several polyphagous parasites (Vosges - June 20-30, 1956)

Host and host plant	C. murinana on fir	C. murinana pupae transferred to artificial leaf-rolls on oak	A. xylosteana & T. viridana on oak
Parasites:			
Tranosema arenicola	Parasitism below 0.1%	-	Parasitism = 12%
Phytodietus polyzonias	Parasitism below 0.1%	-	Parasitism = 15%
Apechthis rufata	No parasitism	Parasitism = 8%	Parasitism = 3%

TABLE 5: Sex ratio of I. maculator emerging from different hosts. (Material from the observation areas in the Vosges and Black Forest (1956). $S.E._m$ = standard error of the samples from C. murinanae and C. murinana)

Hosts	% of ♀	Total number of parasites
Cephalocyota murinanae	49% ($S.E._m = 0.8$)	169
Choristoneura murinana	42% ($S.E._m = 0.06$)	2466
Tachinids:		
Meteorus sp. Tranosema arenicola	Only ♂♂	12
Laboratory breedings on Ephestia kuhniella	Only ♂♂	14

TABLE 6: Sex-ratio of A. rufata at different observation areas and host-plants.

Hosts	♀♀	♂♂
C. murinana, Staufen (1956)	2	8
" Baden-Baden (1956)	4	22
" Slovakia (1956)	-	1
" (CAPEK et al., 1958) (Slovakia)	-	6
" (WIACKOWSKI, 1957) (Poland)	-	4
" Vosges (1956)	-	-
" Transferred to oak, Vosges (1956)	13	-
Tortricids on oak (A. xylosteana, T. viridana) Vosges (1956)	2	3

TABLE 7: Parasitism of corresponding host stages in the fir and spruce budworm

Host stage killed by parasites	Per cent parasitism of the fir budworm (Vosges, 1955-57, S. Black Forest 1956,57)	Per cent parasitism of the spruce budworm (Adirondacks, 1946; Maine, 1949,50)
Eggs (killed by *Trichogramma* sp.)	0 -	0 - 34%
Young larvae (L_3) feeding in the buds (killed by several Chalcids)	- (?)	0 - 16%
Larvae in the 4th and 5th instar (killed by *Apanteles* and *Glypta*)	5 - 20%	8 - 30%
Mature larvae (killed by *Meteorus* and Tachinids)	generally below 1%	16 - 23%
Pupae (killed mainly by Ichneumonids)	20 - 55%	15 - 30%

TABLE 8: Synopsis of the parasite species of C. murinana and C. fumiferana. Species marked with an asterisk are potentially dominant parasites; species in parentheses indicate accidental parasites

Host stage attacked	Parasites of C. murinana	Parasites of C. fumiferana	Parasite group
Eggs	-	Trichogramma minutum	Chalc.
Larvae before hibernation	*Cephaloglypta murinanae	Glypta fumiferanae	Ichn.
	*Apanteles murinanae	*Apanteles fumiferanae	Brac.
	(Apanteles spp.)	(Apanteles spp.)	"
	(?Tranosema arenicola)	Horogenes cacoeciae	Ichn.
Small larvae feeding in buds, etc.	- (?)	Dicladocerus sp.	Chalc.
		Elachertus cacoeciae	"
		Tetrastichus sp.	"
Medium sized and full-grown larvae	Ephialtes (Scambus) inquisitor	(Scambus hispae)	Ichn.
	(Phytodietus ?polyzonias)	*Phytodietus fumiferanae	"
	(Meteorus ruficeps)	Meteorus trachynotus	Brac.
	(Bessa fugax)	-	Tach.
	Blondelia nigripes	-	"
	(Actia maksymovi)	Actia interrupta	"
	-	*Winthemia amoena	"
	(Nemorilla maculosa)	Nemorilla maculosa	"
	-	Phryxe saundersii	"
	(Phryxe nemea)	*Phryxe pecosensis	"
	(Pseudoperichaeta insidiosa)	Pseudoperichaeta erecta	"
	-	*Eumea caesar	"
	-	Clemelis incrassata	"
	-	Ceromasia auricaudata	"
	-	("Erynnia" tortricis)	"
	-	*Lypha setifacies	"
Pupae (rarely full-grown larvae)	Pimpla turionellae	(Pimpla pedalis)	Ichn.
	Apechthis resinator	*Apechthis ontario	"
	(Apechthis rufata)	-	"
	*Itoplectis maculator	*Itoplectis conquisitor	"
	(Itoplectis alternans)	Itoplectis obesus	"
	*Phaeogenes maculicornis	*Phaeogenes hariolus	"
	-	(Exochus sp.)	"
	(Chorinaeus longicornis)	-	"
	(Triclistus globulipes)	-	"
	(Agrypon variitarsum)	-	"
	(Blaptocampus nigricornis)	-	"
	Monodontomerus aereus	(Monodontomerus montivagus)	Chalc.
		(M. ?subobsoletus)	"
	(Amblymerus subfumatus)	(Amblymerus verditer)	"
	(Sarcophagid sp.)	Sarcophaga affinis	Sarcoph.

TABLE 9: Hypothetical evolutionary trends in the fir and spruce budworm and their parasites

Evolution of the Host Species		Evolution of the Parasite Complexes
Common ancestors of *Choristoneura murinana* and *fumiferana*.		Common complex of ecologically and physiologically predisposed but not specialized parasite species.
Topographical separation of the ancient host population, leading to the evolution of vicariant *Choristoneura* spp. in Europe and North America.		Topographical separation of the ancient parasite fauna, leading to the evolution of vicariant parasite species (*Itoplectis* spp., *Ephialtes* spp., *Apechthis* spp., *Phaeogenes* spp., *Horogenes* spp., *Amblymerus* spp., etc.)
Europe: *C. murinana*	North America *Choristoneura* sp.	Slight modifications in the European and American complexes of *Choristoneura* spp.
		Independent specialization of members of the Glyptini, *Apanteles* and *Phytodietus*. Convergent adaptation to the hosts in European and North American Glyptini and *Apanteles* spp.
	Evolution of the sympatric species *C. fumiferana* and *C. pinus* by ecological segregation	Secondary interactions between non-specialized and specialized budworm parasites

RECORD OF THE TACHINID PARASITE *THELAIROSOMA GRACILIS* MESNIL FROM THE COCONUT CATERPILLAR *NEPHANTIS SERINOPA* MEYR. IN INDIA

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The first and only record to date of a Tachinid parasitizing Nephantis serinopa Meyr. in India is that of Ramachandra Rao (1926). Ramachandra Rao et al. (1948) later mentions that while the senior author was examining a severe infestation of Nephantis in the Cochin area in November 1925 he noticed the presence in small numbers of the puparia of a Tachinid, Winthemia sp.*, in the thoracic region of the pupae Nephantis. Although a number of stations have been in existence for several years, particularly for the mass multiplication and liberation of some of the more important hymenopterous parasites of this pest no further records of this Tachinid have been made. Menon and Pandalai (1958) made no mention of any Tachinid parasite of Nephantis.

When the Indian Station of the Commonwealth Institute of Biological Control took up a project on behalf of the Coconut Research Institute of Ceylon to supply parasites of N. serinopa from India but which do not occur in Ceylon, a survey was made in

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*It has been learnt from Ramachandra Rao that the flies reared by him were not in very good condition. Their determination as Winthemia sp. was probably not correct and there is a possibility that they were actually T. gracilis recorded here.

the coconut-growing areas in South India, particularly in the Kerala and Andhra States. During the course of this survey, the Tachinid Thelairosoma gracilis Mesnil was reared from pupae of Nephantis obtained from both the Razole and Ernakulam areas. In the latter area parasitization varied from 2 to 5 per cent.

T. gracilis was first described by Mesnil (1952) from a single male specimen reared by S.N. Chatterjee from Selepa celtis Moore, the larva feeding on Elaeodendron glaucum at Dehra Dun.

This record, made for the first time from Nephantis, indicates the need for a careful survey of all areas infested by the pest, since other parasites whose existence is not known are likely to be found.

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INTRODUCTION OF EXOTIC NATURAL ENEMIES OF SAN JOSÉ SCALE INTO PAKISTAN

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1. Introduction

The San Jose scale, Quadraspidiotus perniciosus (Comst.) (Coccidae : Homoptera), is often a serious pest of fruit trees in certain hill tracts of west Pakistan. Most of these areas are not easily accessible and are agriculturally backward. Chemical control of the pest is rather difficult and expensive. The Government of Pakistan desired, through the Plant Protection Department, Karachi, that an attempt should be made to control it biologically. The Pakistan Station, Commonwealth Institute of Biological Control, Rawalpindi, was therefore requested to attempt the introduction of some of the exotic natural enemies of this pest. Suitable arrangements were made and importation of parasite material and laboratory multiplication started in August 1959. It was arranged that field releases of parasites and recovery check-ups were to be carried out by local agricultural authorities in the areas concerned, except in the Murree Hills where these were also carried out by the staff of the Pakistan Station.

This paper includes information collected during the course of this work on the pest and its natural enemies together with an account of the breeding methods employed and the results achieved up to the end of 1960.

2. Distribution of San Jose scale

A study of the distribution of San Jose scale in West Pakistan and the location of heavy infestations was necessary in order to select suitable sites for the release of exotic natural enemies. Infestations were found at Parachinar (Kurram agency), in some Galis in the Hazara district, in the Murree hills and at Rawalakot, Dhirkot, Chamyati, Chamankot and Bagh (Azad Kashmir).

The pest is also known to occur in some parts of Baluchistan (Isaac, 1932-33) and at Wana in South Waziristan. Pruthi and Batra (1938) recorded it from Kurram valley, Abbottabad and Mansehra and Rahman (1940) reported it from Peshawar. These places, however, have not yet been surveyed by us.

Since the release of parasites in the Murree hills was to be carried out by staff from this Station, the occurrence of the pest in this area was studied in greater detail and heavily infested localities selected as release points together with the sites.

3. Host plants and damage

San Jose scale is said to attack some 700 different plants in various parts of the world (Rimes, 1959). In Pakistan we found that it causes considerable damage to a number of fruit trees including apple (Malus pumila Mill.), pear (Pyrus communis L.), peach (Prunus persica Stokes) and plum (Prunus bokhariensis Royle). In addition, heavy infestations were observed on Rosa sp. at Parachinar and in the Murree hills, especially on bushes growing near infested fruit orchards. Young plants, especially, were

severely attacked and usually died. Orchardists were often seen destroying such plants. The scales occurred on almost all parts of the infested plants with frequent heavy concentrations on the lower portions.

4. Endemic natural enemies

The following predators and parasites were found during the course of this survey:

Predators

Coleoptera

Coccinellidae

(i) Coccinella 7-punctata L.: A common predator which is known to prey upon a wide variety of insects. Both the adults and larvae attacked the pest in all the infested orchards and localities visited.

(ii) C. 7-punctata L. var. divaricata Wse.: This was observed in small numbers in C. 7-punctata populations.

(iii) Chilocorus infernalis Muls.: Adults and larvae were found feeding on the pest in the Murree hills and at Rawalakot, especially at the beginning of the season.

(iv) Pharoyscymnus flexibilis Muls. : A good predator, both in the larval and adult stages, was recorded from Rawalakot and the Murree hills.

(v) Adalocaria hexaspilota Hope : Adults were collected from young apple trees infested with San Jose scale in the Murree hills.

(vi) ? Gen. et sp. indet.: Larvae were collected from apple trees infested with San Jose scale at Rawalakot.

Nitidulidae

(vii) Cybocephalus sp.: Both adults and larvae were found feeding on San Jose scale on apple trees in the Murree hills.

Parasites

Hymenoptera

Aphelinidae

(viii) Coccophagoides sp.: This was reared from San Jose scale from roses at Parachinar.

(ix) Aphytis sp. - proclia group: A very common parasite with high degree of parasitism was recorded from the Murree hills. During the season the adults could be seen crawling all over the infested twigs of apple trees.

(x) Azotus sp.: This parasite was reared from San Jose scale from roses at Parachinar.

5. Exotic natural enemies selected for introduction

In view of the performance of some of the natural enemies of this scale in other parts of the world and their absence from this region, the parasites Prospaltella perniciosi Tower and Aphytis diaspidis (Howard) and the predator Chilocorus kuwanae Silv. were selected for trial introductions. P. perniciosi was the first parasite to be imported and tried. Work has, therefore, so far been mainly confined to this species.

6. Breeding of the host

In order to breed San Jose scale in the laboratory citron melons (Citrulus vulgaris var. citroides), used as laboratory host elsewhere (Flanders, 1944), were successfully grown at the Station site from the seeds imported from California. In 1959 good crops of melons were obtained under Rawalpindi conditions and more than seven tons of fruit were gathered from an area of about half an acre. Unfortunately the storage conditions with high temperatures and excessive humidity during a part of the year adversely affected their keeping quality. A quick deterioration of melons resulting in yellowing, rotting and fungus spotting was observed. Banana squash (Cucurbita maxima), used by Dr D.C. Lloyd of our Californian Station, did not grow well under Rawalpindi conditions. However, along with the use of citron melons the local cucurbits were also tried. Although San Jose scale could grow on a variety of cucurbits it flourished very well on musk or melon pumpkin (Cucurbita moschata) and a local variety of common or Spanish gourd (C. maxima). Their keeping quality was very good. Selected healthy fruits have maintained thriving cultures of scale in the laboratory for over a year. This point is very important since these cucurbits are neither grown in this region nor are available in the market throughout the year. Light coloured, small sized, healthy and solid fruits proved quite satisfactory for breeding San Jose scale.

To start laboratory cultures a few crawlers were obtained from San Jose scale females on apples at Murree and all further propagation was carried out from this initial nucleus culture. Separate rooms

were used for culturing scales and breeding parasites. Crawlers were removed from mother scale cultures at short intervals, usually three times a day. It was found that if these were removed only once a day or at longer intervals, many of them settled on the mother culture fruit with a resulting low recovery of crawlers and in considerable reduction in the numbers settling successfully on fresh fruits.

Blowing was found to be a convenient and satisfactory method of crawler collection. The crawler-producing fruit was placed on butter paper and light puffs of air were blown over it through rubber tubing, the air-stream being directed downwards and the butter paper being lifted on the side being blown to prevent crawlers falling off the paper (Fig. 1). After blowing the fruit was removed and the crawlers were brought together in the centre of the butter paper by gentle tapping. These were then placed on a fresh fruit kept in a settling box (Fig. 2) by inverting the paper over the fruit and tapping it lightly from above. The box was then closed and kept dark to enable the crawlers to settle uniformly all over the surface of the fruit. After about 24 hours the infested fruits were removed from the settling box and were placed on racks (Fig. 3) until the scales were of a suitable size for parasitization.

7. Multiplication of exotic natural enemies

The following three types of cages were used for rearing parasites:

(i) These consisted of four pieces of sheet glass, usually 14" x 12", joined together by specially made tightly fitting aluminium

corners to form a cubical or rectangular structure depending upon the size of the glass plates used. Paper strips were pasted on the inner and outer vertical sides of this structure in between the upper and lower aluminum corners. The bottom was a plain wooden board on which a layer of thin cotton cloth covered with tissue paper was placed. The thickness of the upper edges of the glass plates was brought into line with the thickness of the aluminum corners by pasting on them cardboard strips of the same thickness. The top was covered with voile cloth held in position by an elastic band (Fig. 5). Such cages were advantageous in that they could be assembled and dismounted in short order. Moreover, cages of any size could be constructed just by putting in glass sheets of the desired size.

(ii) Cages similar to the above but having only the front of the glass and fixed plywood on the other three sides and the bottom were also employed (Fig. 4).

(iii) Sleeve cages as used at the University of California for rearing parasites (Peterson, 1947) were modified to have a tightly fitting removable top instead of a fixed one with a side door. These were not very convenient and hence were rarely used.

A fruit with healthy scales of suitable age was placed in the cage and a glass tube open at both ends having 50 to 100 or more adults of P. perniciosi depending upon the number of hosts to be parasitized, was placed on the darker side of the fruit with one upper end resting upon it (Fig. 6). The parasites then crawled out on the scales. Scales used for parasitization were 3-12 days old but maximum parasitization was obtained when they were 5-7 days

old. A strong source of light attracted the parasites towards it and darkness reduced parasitization, but fairly strong diffused light seemed to be ideal. When all the adult parasites had died and a number of the scales were parasitized the fruit was removed and placed on a rack for development of the parasite progeny. Flanders (1944) recorded a minimum developmental period of 19 days and observed that this was prolonged if the first, youngest, stages of the host were attacked. In our rearings this period varied between 19 and 33 days depending upon temperature, humidity and probably on the age of the host. A few observations in this connection are noted below.

S.No.	Age of scales in days	# Temperature (°F.)				#Relative humidity (Per cent)		*Period of development in days
		Maximum		Minimum				
		Range	Mean	Range	Mean	Range	Mean	
1	6	83-87	84.4	80-83	80.4	62-84	77.5	19
2	5-6	82-86	84.0	78-82	80.9	62-84	76.4	20
3	7-10	78-87	83.6	72-83	80.2	60-84	76.0	21
4	1-4	82-90	85.5	75-87	81.8	62-80	74.0	24
5	7	74-83	79.8	68-80	71.8	70-83	76.1	31
6	6	74-81	77.8	68-76	70.7	65-95	76.1	33

Temperature and humidity records pertain to the period begining with the liberation of crawlers to the emergence of parasites.

* From the date of release of parasites for parasitization to the first emergence of their progeny.

A few days prior to the emergence of the parasites the fruit infested with the parasitized scales was placed in an emergence cage (similar to that used for parasitization). The emerging parasites were collected in an aspirator (Fig. 7) once or twice a day. The

parasites were sucked up very lightly; strong suction carried them to the nylon covered end of the glass tubing of the aspirator with consequent possibility of damage. The distal end of the aspirator was kept a little way from the fruit to avoid crushing the parasitized scales. When the desired number of parasites had been collected in the aspirator both the sucking and the collecting tubes together with their corks were removed and replaced with a cork on one end and voile cloth on the other and another piece of glass tube was used for further collection, the process being repeated until all the adult parasites were collected.

A small piece of butter paper, slightly bigger than the diameter of the tube and bearing fine streaks of honey, was inserted into the tube to provide food for the adult parasites.

During the course of these operations up to 10,600 adult parasites were collected from a single infested fruit over a period of four months. The scales were exposed to parasitization only once, at the beginning of the process, while later parasitism occurred from subsequent progeny since usually when the adult parasites emerged some scales of suitable age were available for parasitization and, before the emerging parasites were removed, some of the scales had already been parasitized and these gave rise to a further generation. Hence after the first parasitization automatic propagation of both host and parasite on the same fruit continued for a long period without any further effort.

A similar method was used for the multiplication of A. diaspidis with the only modification that the host (San Jose scale) offered

for parasitization was about 30 days old.

Breeding of C. kuwanae was very simple. Adults were liberated in cages containing San Jose scale cultures on fruits bearing all stages of the scale.

8. Field releases

The following two methods were adopted in liberating parasites.

(i) In sleeves: At the beginning parasites were released in voile sleeves placed on the scale-infected plants in order to restrict parasite movement and to afford protection from adverse weather conditions. For a sleeve, three rings of equal size of steel wire or tender twigs were placed round the part of the plant to be sleeved. Three sticks were tied to the rings to form a cylindrical frame. Voile cloth was then wrapped around this, the edges being rolled and roughly stitched, and the cylinder so formed extended beyond the frame at the ends. The lower end was tied around the plant and after the release of the parasites in the sleeve, the upper end was also tied to the same branch (Fig. 8). The sleeve could be removed when the parasites were dead.

(ii) In the open: The tubes containing adult parasites were tied or taped to an infested portion of the plant and were opened at both ends to allow the parasites to crawl out slowly (Fig. 9).

Prior to making a release it was ascertained that all stages of the scale were present on the selected plants, particularly those stages attacked by the particular parasite species, and also that no chemical insecticides had been recently used.

During the period August to November 1959 28 sleeves were put out by the staff of this Station at four places in the Murree hills (Rewat (11), Dewal (5), Khanitak (3) and Morah Sharif (1)) and at two places in Kashmir (Rawalakot (6) and Chikar (2)), whilst a further 25 sleeves were put out in Kashmir (Rawalakot (19), Khirk (4), Pathri (1) and Hurnomorah (1)) by local agricultural authorities. Parasites were often liberated repeatedly in the same sleeve.

Fruits bearing a large number of parasitized scales were supplied to agricultural officers at Parachinar (12), Hazara district (14), Kashmir (14) and Gilgit (9) for release of adult parasites in their respective areas.. Some of these officers were given a short period of training.

During the year 1960 18 open releases of P. perniciosi were made at four localities in the Murree hills (Khanitak, Dewal, Aliot and Rewat).

Five releases of A. diaspidis, consisting of more than 1,000 adults, were made at Rewat and one of C. kuwanae, comprising about 40 adults, at Khanitak.

9. Recovery of parasites

In May 1960 P. perniciosi was recovered from infested apple twigs from Khanitak and Dewal and again in October 1960 from Khanitak, places where releases were made in 1959. Thus the parasite appears to have been established at these two localities at least. Results of 1960 releases will be checked in the spring of 1961 when

the snow clears.

Summary

Work on the biological control of San Jose scale during the period August 1959 to December 1960 has been described.

Occurrence and distribution of the pest in the Murree hills was studied. Six species of Coccinellidae, one species of Nitidulidae and four species of Aphelinidae were recorded as native natural enemies of the pest in this region.

The exotic natural enemies, P. perniciosi, A. diaspidis and C. kuwanae, were selected for trial introductions into West Pakistan. The work so far, however, has been confined mainly to the first of these species. Methods used for breeding San Jose scale and its parasites have also been described. The parasites were released at five different sites in the Murree hills by the staff of the Station and material for releases in other areas was supplied to the agricultural officers concerned. Recovery check-ups showed that P. perniciosi was established in at least two localities in the Murree hills. A few releases of the other species of natural enemies were also made.

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Fig. 1 (*above*)
Crawler collection by blowing

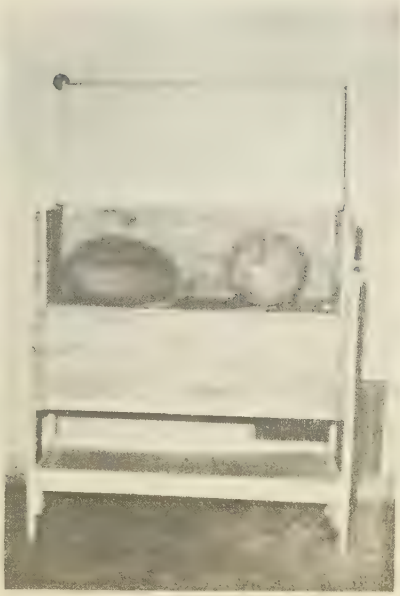


fig. 2 (a)

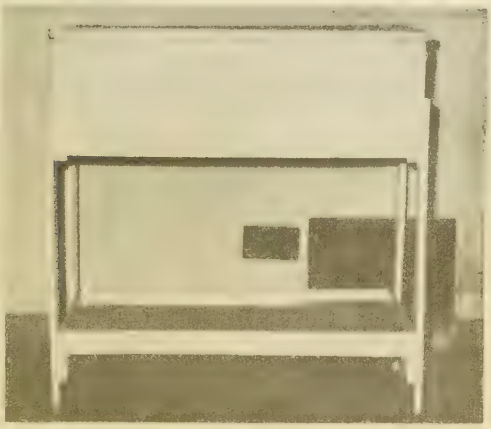


fig. 2 (b)

Fig. 2 (*above*)
Crawler settling box, open (*a*), closed (*b*)

Fig. 3 (*below*)
Racks for storing San Jose scale infested cucurbit fruits

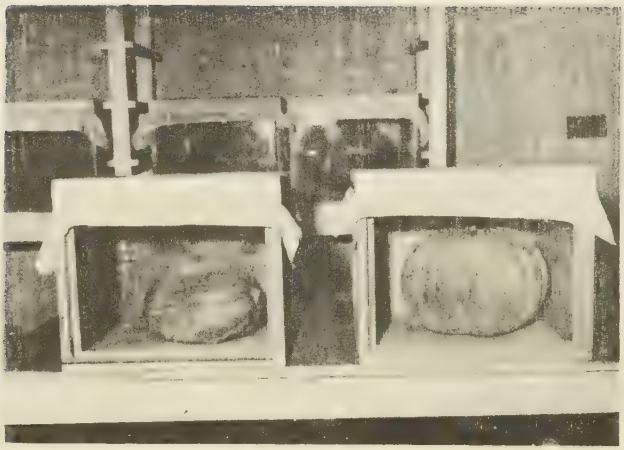


Fig. 4 (*left*)
Plywood cages with front glass

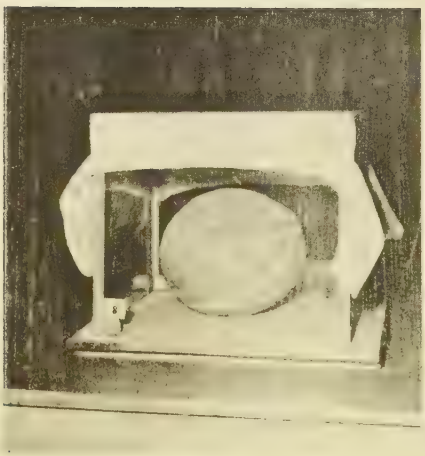


fig. 5 (*a*)

Fig. 5
Glass cages (*a*), one corner enlarged (*b*)

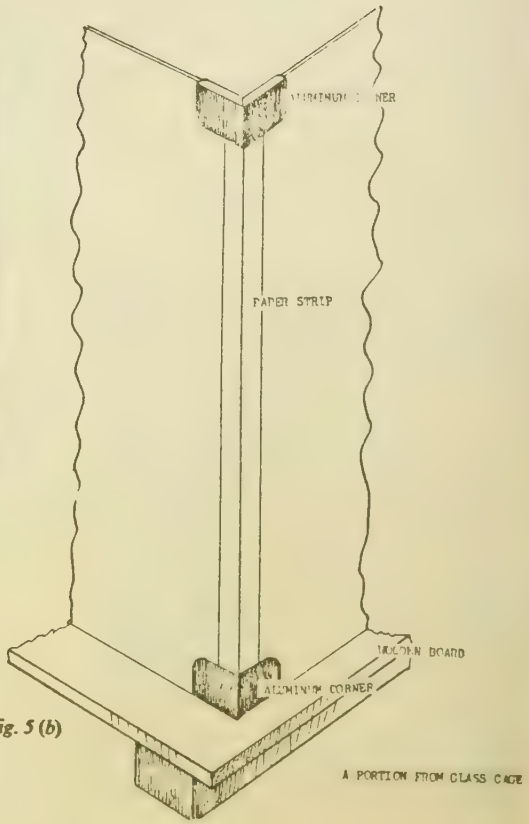


fig. 5 (*b*)

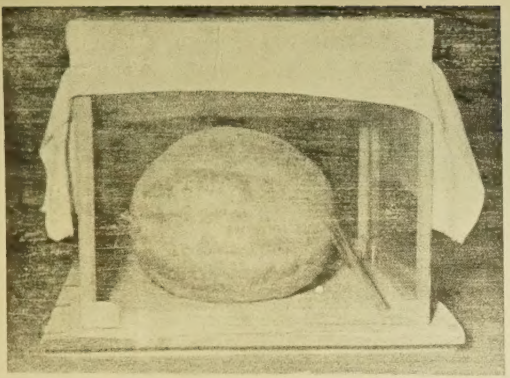


Fig. 6 (left) Liberation of parasites on San Jose scale infested cucurbit fruit for multiplication

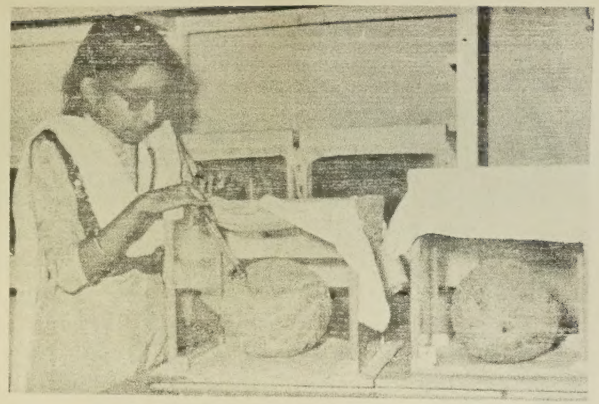


fig. 7 (b)

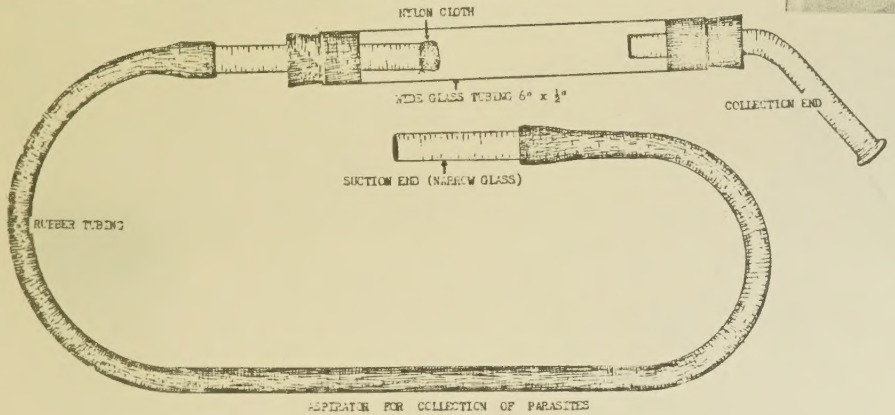
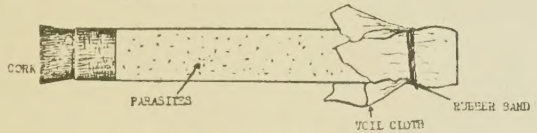


Fig. 7
Aspirator for collection of parasites (*a*), parasites being collected (*b*)

fig. 7 (a)



A TUBE CONTAINING PARASITES FOR RELEASE.

Fig. 8 (*left*)
Release of parasites : parasites liberated in cloth sleeve on infested branch

Fig. 9 (*right*)
Release of parasites : tube containing parasites tied to an infested branch